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Blocking and guiding adult sea lamprey with pulsed direct current from vertical electrodes

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ABSTRACT

Controlling the invasion front of aquatic nuisance species is of high importance to resource managers. We tested the hypothesis that adult sea lamprey (*Petromyzon marinus*), a destructive invasive species in the Laurentian Great Lakes, would exhibit behavioral avoidance to dual-frequency pulsed direct current generated by vertical electrodes and that the electric field would not injure or kill sea lamprey or non-target fish. Laboratory and in-stream experiments demonstrated that the electric field blocked sea lamprey migration and directed sea lamprey into traps. Rainbow trout (*Oncorhynchus mykiss*) and white sucker (*Catostomus commersoni*), species that migrate sympatrically with sea lamprey, avoided the electric field and had minimal injuries when subjected to it. Vertical electrodes are advantageous for fish guidance because (1) the electric field produced varies minimally with depth, (2) the electric field is not grounded, reducing power consumption to where portable and remote deployments powered by solar, wind, hydro, or a small generator are feasible, and (3) vertical electrodes can be quickly deployed without significant stream modification allowing rapid responses to new invasions. Similar dual-frequency pulsed direct current fields produced from vertical electrodes may be advantageous for blocking or trapping other invasive fish or for guiding valued fish around dams.

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1. Introduction

Sea lamprey (*Petromyzon marinus*), a hematophagic ectoparasite native to the Atlantic Ocean, invaded the upper Laurentian Great Lakes in the 1930s and triggered fishery collapse and ecosystem dysfunction (Smith and Tibbles, 1980). Sea lamprey control in the Great Lakes is the foundation for a fishery valued at 7 billion U.S. dollars annually (ASA, 2008). The integrated control program uses three techniques: dams and low-head barriers limit the amount of spawning habitat available; traps remove adults to reduce reproductive potential; and selective pesticides kill larvae produced by those adult sea lampreys that avoid traps and find suitable spawning habitat (Christie and Goddard, 2003). Development of versatile, low impact technologies to limit access to spawning habitat would further improve sea lamprey control.

Alternating current (AC) was first used to block and guide sea lamprey (Baker, 1928; Applegate et al., 1952), but resulted in excessive non-target fish mortality (Erkkila et al., 1956) because the electric field polarity rapidly reverses (Reynolds and Kolz, 2012). Soon after, pulsed direct current (PDC) was successfully used to block upstream spawning migrations of sea lamprey (McLain, 1957). PDC is now typically used for fish blockage because the field is not continuous and polarities do not reverse, thus the likelihood of injury is reduced (Reynolds and Kolz, 2012).

Although vertically suspended electrodes were first used for sea lamprey control (McLain, 1957), most PDC fields are now produced by horizontal electrodes mounted on the stream bottom to shelter electrodes from stream debris. The primary difference between vertical and horizontal electrodes is the plane in which the electric field intensity varies. Horizontal electrode fields vary on the vertical plane – the electric field is most intense near the substrate (electrodes) and decreases in intensity near the surface of the water. Vertical electrode fields vary on the horizontal plane; field intensity decreases as horizontal distance from the electrode increases.

The effectiveness and application of electric fields to modify fish behavior may be limited when using horizontal electrodes mounted across the stream bottom. Electric fields generated from bottom-mounted electrodes are weaker at the water surface than at the bottom. During floods, the upper water column may not be sufficiently electrified to block fish. Installation of bottom-mounted electrodes also requires stream channel modifications, ultimately limiting rapid response to new invasions. PDC fields generated by vertical electrodes may be more effective and versatile for blocking and guiding fish. Vertical electrodes may be more effective at blocking fish because the field does not weaken with depth. Vertical electrodes could also be quickly deployed without significant stream modification allowing rapid responses to new invasions.

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We tested the hypothesis that sea lamprey would exhibit behavioral avoidance to a vertical electrode PDC field (hereafter, VE-PDC field) and that the field would not injure or kill sea lamprey or non-target fish. In contrast to the single-frequency PDC waveform used in early sea lamprey control programs (3 Hz frequency, 66% duty cycle; McLain, 1957), we tested dual-frequency PDC that consisted of "packets" of brief pulses at high frequency, each packet delivered at low frequency, resulting in low duty cycle and power requirement (Reynolds and Kolz, 2012; refer to Section 2 for a detailed description of the waveform). Given our hypothesis and the needs of the current sea lamprey control program, we predicted that (1) the behavioral avoidance of adult sea lamprey to VE-PDC fields would be sufficient to block and (2) direct them into free-standing traps and that (3) even when sea lamprey and non-target species are subjected to the electric field, they would not be injured or killed.

2. Methods

2.1. Laboratory experiments

2.1.1. General description

Laboratory studies were conducted in a raceway (5.0 m × 1.85 m observation area) at United States Geological Survey, Great Lakes Science Center, Hammond Bay Biological Station (HBBS), Millersburg, MI, to identify candidate electric field settings in a natural stream application. Detailed methods are provided in the supplemental material (S1, Tables S1 and S2, Fig. S1 and S2).

2.2. General procedures for in-stream experiments

2.2.1. Experimental stream

VE-PDC fields were tested in a 500 m reach of the Ocqueoc River, MI, USA, during May–July 2012. The test site lacked AC power and was located 1 km from the nearest road. The experimental reach was about 10 km upstream of a sea lamprey barrier. A site with no sea lamprey infestation was advantageous because the number of sea lampreys in the system could be controlled.

The upstream portion of the experimental site was characterized by the confluence of Silver Creek and the Ocqueoc River, which allowed multiple blocking and trapping scenarios to be tested. The confluence was mapped to a resolution of 1 m^2 according to the deflection traverse method (McMahon et al., 1996). While mapping, a 1 m^2 visual grid system was established by arraying synthetic twine on transect lines over the stream channel. Grid lines were georeferenced (Fig. 1A and B; Trimble GeoExplorer 3000 Series GeoXH, Sunnyvale, CA) and displayed on the stream map. The physical structure of the stream channel was characterized by measuring depth and water velocity in the middle of each square meter as displayed on the stream map (Fig. S3). Discharge rating curves (McMahon et al., 1996) were developed for both Silver Creek and Ocqueoc River using weekly discharge estimates taken at points 20 m upstream of the confluence in each stream. Stream gauge heights in Silver Creek and the Ocqueoc River were recorded before each trial and the rating curves were used to estimate discharge during each trial. Ambient conductivity and temperature were recorded with loggers (Hobo U24-001-Conductivity Logger, Onset Co, Bourne, Massachusetts) every 15 min during experimentation in Silver Creek and the Ocqueoc River 20 m upstream of the confluence.

2.2.2. Experimental animals

Sea lamprey were collected in traps fished in tributaries to northern Lake Michigan and Lake Huron by the United States Fish and Wildlife Service (USFWS), Marquette Biological Station and the Department of Fisheries and Oceans, Sea Lamprey Control Center and were maintained at HBBS in 1000 L tanks supplied with Lake Huron water at ambient temperature, which ranged from 6 to 16 °C. Only female sea lampreys were used in behavioral assays to prevent infestation of the upper Ocqueoc River. Pre-ovulatory females were used instead of ovulatory females because they actively migrate upstream in search of spawning habitat. Females used in field experiments averaged 208 g (range 116–322 g) in weight and 454 mm (range 390–540 mm) in length.

Pre-ovulated females were implanted with uniquely-encoded 32 mm passive integrated transponders (PIT tags, Oregon RFID, Portland, Oregon) between 10 and 14 h prior to release in the Ocqueoc River. PIT tags were inserted in the abdomen through a 3 mm incision. Immediately after tagging, sea lampreys were transported to the Ocqueoc River in aerated tanks and placed in an acclimation cage (1 m^3) about 500 m downstream of the confluence of Silver Creek and the Ocqueoc River.

2.2.3. Vertical electrode guidance system

Use of VE-PDC at the confluence of Silver Creek and the Ocqueoc River was approved by the Michigan Department of Environmental Quality through permit number 12-71-0004-P. The VE-PDC fields were generated with electrodes and two pulsators developed by Procom Systems (Wroclaw, Poland) and distributed in North America by Fishways Global LLC (Livonia, MI). Vertical electrodes were installed with no stream modifications. Installation of any electric field design described herein took three people less than 3 h. Each pulsator weighed 27 kg and drew between 200 and 400 W depending on the electric field size and intensity. Both pulsators were powered with a gas 3000 W generator (Honda EU3000iS Inverter, Georgia, Alpharetta).

At the desired fish guidance location, symmetric VE-PDC fields were produced by a line of negative electrodes between two lines of positive electrodes. The upstream line of positive electrodes produced a PDC field to guide downstream migrating non-target fish away from the highest voltage gradients. The downstream line of positive electrodes produced a PDC field to guide upstream migrating fish, in this case sea lamprey, away from the highest voltage gradients. Positive electrodes (stainless steel pipes 30 mm diameter and 1 m long) and negative electrodes (stainless steel pipes 20 mm diameter and 1 m long) were suspended in the stream using overhead stainless steel cables (6 mm diameter). Specific details concerning the length and spacing of electrodes for each experiment are presented in supplemental figures. During in-stream experiments, electric fields were dual-frequency PDC. Each group (packet) of pulses consisted of five 1.8 ms pulses with four 8.2 ms off-periods in between for a total duration of 41.8 ms. The duration from the start of one group to the next was 100 ms. Several electric field design configurations were tested (blocking and trapping experiments) and the voltage gradient in the water was modified by moving lines of electrodes, adding electrodes, or increasing the voltage supplied to the electrodes.

Electrode locations for each electric field design were geo-referenced to the stream map (Trimble GeoExplorer). The voltage gradient ($V\,cm^{-1}$; peak values, not the average of one on-off cycle) produced by each electric field design was measured with a 10 cm prove (voltage measured over a 10 cm distance and divided by 10) connected to an oscilloscope (Tektronix TPS2000B Digital Storage Series, Tektronix Co, Beaverton, Oregon), geo-referenced, and displayed on the stream map. Specifically, voltage gradient was measured along a transect halfway between the line of positive and negative electrodes at every 0.5 m for each electric field design tested (see supplemental figures for measurement locations and values).

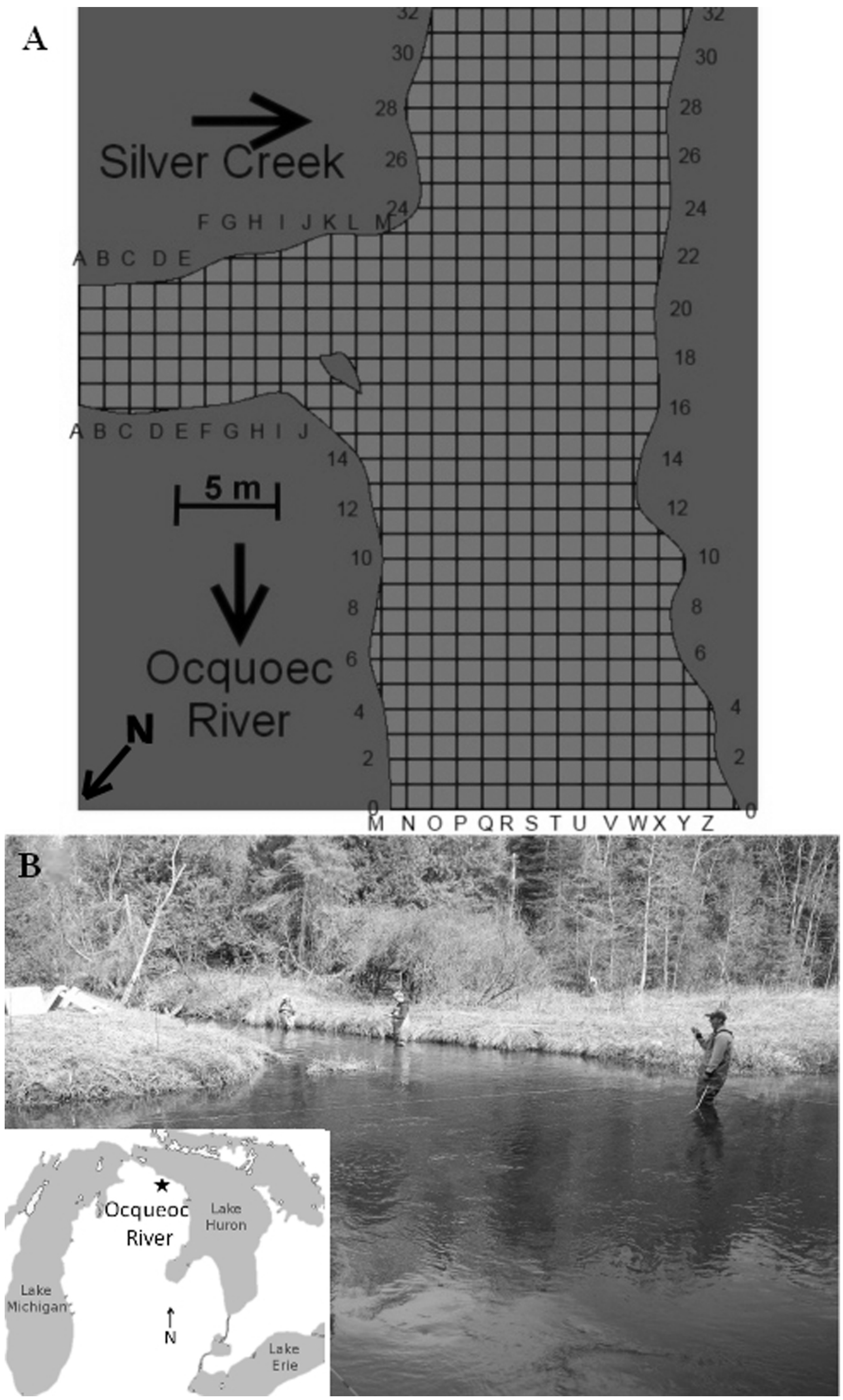

Fig. 1. The confluence of Silver Creek and the Ocqueoc River which was used to determine if a vertical electrode pulsed direct current field can block and guide sea lamprey migration. Stream map illustrating grid system developed to map sea lamprey movements, electrode placement, and in-stream voltage gradients (A). Picture of confluence of Silver Creek and the Ocqueoc River taken while mapping the stream and laying out stream grid system (B). Regional map illustrates location of Ocqueoc River. The study site was located at latitude 45.4525° and longitude −84.0749°.

2.3. Methods to test prediction 1: A VE-PDC field will block sea lamprey migration

2.3.1. Procedures

To determine if a VE-PDC field can block adult sea lamprey migration into spawning tributaries, 40 female sea lampreys were released per trial under four electric field settings: (1) electric field off (control), (2) Silver Creek electric field on (block migration into Silver Creek), (3) Ocqueoc River electric field on (block migration into Ocqueoc River), and (4) Ocqueoc River and Silver Creek electric field on (block upstream migration in both tributaries). The average voltage gradient measured along a transect midway between positive and negative electrodes was 3.3 V cm^{-1} (SD = 1.0, voltage applied to electrodes = 110 V) in Silver Creek and 3.7 V cm^{-1} (SD = 0.8; voltage applied to electrodes = 110 V; Fig. S4) in the Ocqueoc River. The average power density (peak voltage gradient squared times ambient conductivity) along a transect midway between positive and negative electrodes was 3.75 mW/cm^3 in Ocqueoc River and 3.54 mW/cm^3 in Silver Creek.

PIT-tagged sea lampreys were released from the holding cage at 2100 h and their upstream migration patterns were monitored until 0600 h the following morning using PIT antennas (Oregon RFID, Portland, Oregon). Experiments were conducted at night because sea lamprey are nocturnal during their spawning migration (Applegate, 1950). The number of sea lampreys that approached the confluence and moved downstream from the confluence was determined using two cross-channel PIT antennas (direction of movement could be determined) located 50 m downstream of the confluence. To ascertain sea lamprey stream selection, PIT antennas were placed in Silver Creek and the Ocqueoc River 20 m upstream of the confluence. In all experiments, PIT antennas were tested and tuned before each trial to ensure the read range was greater than 0.5 m from the antenna wire.

Experiments to block sea lamprey migration occurred from 14 May 2012 to 16 June 2012. In all in-stream experiments described, electric field treatment selection for each trial was determined by a random number generator. During experiments to block sea lamprey migration in Silver Creek, discharge ranged from 0.18 to 0.49 cms (mean 0.25 cms); temperature at 2200 h ranged from 10.3 to 20.4 °C (mean 15.8 °C) and ambient conductivity at 2200 h ranged from 250.3 to 370.9 μS cm^{-1} (mean 325.5 μS cm^{-1}). In the Ocqueoc River, discharge ranged from 1.04 to 1.46 cms (mean 1.17 cms), temperature at 2200 h ranged from 11.5 to 23.1 °C (mean 17.6 °C) and ambient conductivity at 2200 h ranged from 238 to 301.6 μS cm^{-1} (mean 273.6 μS cm^{-1}). Temperature and conductivity were reported at 2200 h because that was when most sea lampreys approached the confluence. To determine if variability in the proportion of sea lampreys approaching the confluence in each trial was explained by electric field treatment or Ocqueoc River water temperature, a binomial generalized linear model (i.e. logistic regression) was fit to the data. The logistic regression model showed no evidence of overdispersion and no significant nonlinearities were observed when evaluated with generalized additive models with cubic splines.

Sea lampreys that approached the confluence during the trial were assigned to one of four categories based on their initial movement pattern at the confluence: (1) moved upstream of the confluence in the Ocqueoc River, (2) moved upstream of the confluence in Silver Creek, (3) did not move upstream of the confluence, but reversed migration after approaching the confluence, or (4) did not move upstream of the confluence, but settled upstream of the PIT antenna located 50 m downstream of the confluence. For example, a sea lamprey would be categorized as moved upstream of the confluence in the Ocqueoc River if on its first approach to the confluence was detected on the PIT antenna upstream of the confluence in the Ocqueoc River, even if later that night it reversed migration. Because no sea lamprey were observed moving upstream of the confluence of Silver Creek and the Ocqueoc River during some electric barrier treatments, exact binomial confidence intervals (CI; Clopper and Pearson, 1934) were used to describe the upper confidence limit for zero probabilities of movement upstream in Silver Creek and the Ocqueoc River. To determine if the proportion of sea lampreys reversing migration and settling near the confluence varied among treatments, a mixed effect binomial generalized linear model was used where the fixed effect was electric barrier treatment and random effect was trial date. All statistical analyses reported in this manuscript were conducted in R (Version 2.3.1; R Development Core Team, 2009).

2.4. Methods to test prediction 2: A VE-PDC field will guide sea lamprey into a trap

2.4.1. Procedures

VE-PDC fields were tested as a non-physical lead to guide sea lamprey into traps in Silver Creek and the Ocqueoc River. During each trial, the electric field was activated from 2100 to 0100 h and 40 PIT-tagged female sea lampreys were released at 2100 h and tracked until 0100 h the following morning. Trials were terminated at 0100 h because very few sea lampreys were observed between 2400 and 0100 h. Sea lampreys were removed from the trap at 0100 h and PIT tag IDs were verified. PIT antennas were placed farther away from the confluence during trapping trials because the electromagnetic field generated by the electrodes interfered with the PIT system. Two PIT antennas were placed (1) 150 m downstream of the confluence to determine approaches to and reversals from the confluence, (2) 50 m upstream in Silver Creek to determine upstream movement in Silver Creek, and (3) 50 m upstream of the confluence in the Ocqueoc River to determine upstream movement in the Ocqueoc River. During all trapping trials, the voltage gradient was less than 0.1 V cm^{-1} at the entrance of the trap and less than 0.01 V cm^{-1} within the trap. Traps were electrically shielded using galvanized steel 0.30 mm mesh hardware cloth.

From 2200 to 0100 h technicians observed sea lamprey movements near the trap by illuminating the water with red light. Individual sea lamprey movement tracks were drawn on the stream map referencing the map grid system. Afterwards, sea lamprey movement tracks were digitized in Python (Version 2.5.4, http://www.python.org/, Python Software Foundation) and Python Imaging Library (Version 1.1.7, http://www.pythonware.com/) and exported to Paint.NET (Version 3.5.10, http://www.getpaint.net/) for final display on the stream map. Movements of individual sea lamprey may have been recorded multiple times during a trial because they did not have unique external identifiers.

Experiments to trap sea lamprey occurred from 16 June 2012 to 20 July 2012. During trapping experiments in Silver Creek, discharge ranged from 0.15–0.25 cms (mean 0.18 cms), temperature at 2200 h ranged from 16.9–21.4 °C (mean 19.2 °C), and ambient conductivity at 2200 h ranged from 331.1–391.1 μS cm^{-1} (mean 369.6 μS cm^{-1}). In the Ocqueoc River, discharge ranged from 1.97–1.27 cms (mean 1.04 cms), temperature at 2200 h ranged from 18.3–23.5 °C (mean 21.3 °C), and ambient conductivity at 2200 ranged from 278.8–322.4 μS cm^{-1} (mean 301.7 μS cm^{-1}).

2.4.2. Test 1: Silver Creek trapping

Sea lamprey were directed into Silver Creek by an electric field arrayed across the Ocqueoc River at a 30° angle toward the entrance of Silver Creek. A 69 cm × 99 cm fyke net with 7 cm mesh size (H. Christiansen Co. Minnesota, Duluth; with no leads) deployed against the right bank of Silver Creek (as determined by looking upstream) was used to capture sea lamprey. An electric field arrayed from the left corner of the trap funnel at a 30° angle downstream to the left bank was used to guide sea lamprey to the trap (Fig. S5). The average voltage gradients measured along a transect halfway between positive and negative electrodes in Silver Creek and the Ocqueoc River were 2.4 V cm^{-1} (SD = 0.5; 88 V applied to electrodes in Ocqueoc River; 66 V applied to electrodes in Silver Creek; Fig. S5). The average power densities along a transect between positive and negative electrodes in Silver Creek and the Ocqueoc River were 2.1 and 1.7 mW/cm^3, respectively. During Silver Creek trapping trials, a technician described each sea lamprey location (referencing the stream map grid system from transects K through A; Fig. 1A), to another technician who recorded movement tracks on the stream map.

Five trials were conducted when the electric fields were on and four trials were conducted when the electric fields were off. Logistic regression was used to determine if variability in the proportion of sea lampreys approaching the confluence each night was explained by electric field treatment or Ocqueoc River water temperature. Sea lampreys that approached the confluence were assigned to one of five categories based on their initial movement pattern at the confluence: (1) moved upstream of confluence in the Ocqueoc River, (2) moved upstream of confluence in Silver Creek, (3) captured in Silver Creek trap, (4) did not move upstream of confluence, but reversed migration after approaching the confluence, or (5) did not move upstream of confluence, but settled upstream of the PIT tag antenna downstream of the confluence. Because no sea lamprey were trapped when the electric fields were off, exact binomial CIs were used to describe the upper confidence limit for trap efficiency estimates. To determine if the proportion of sea lampreys moving upstream of the confluence in Silver Creek, moving upstream of the confluence in the Ocqueoc River, reversing migration, and settling near the confluence differed significantly between treatments, a mixed effect binomial generalized linear model was used where the fixed effect was electric barrier treatment and random effect was trial date.

2.4.3. Test 2: Ocqueoc River trapping

In the Ocqueoc River, a 1 m × 2 m fyke net with 8 cm mesh size (H. Christiansen Co. Minnesota, Duluth; with no leads) deployed against the right bank of the Ocqueoc River (as determined by looking upstream) was used to capture sea lamprey. A VE-PDC field arrayed from the left corner of the trap funnel at a 45° angle downstream to the left bank was used to guide sea lamprey to the trap (Fig. S6). The electric field for guiding sea lamprey to a trap in the Ocqueoc River was tested at four settings; off, low (67 V applied to electrodes), medium (88 V), and high (108 V). The average voltage gradients measured along a transect halfway between positive and negative electrodes at low, medium, and high settings were 2.2 (SD = 1.1), 3.0 (SD = 1.1), 4.0 (SD = 1.4) V cm^{-1}, respectively (Fig. S6). The average power densities at low, medium, and high settings along that transect were 1.5, 2.7, and 4.8 mW/cm^3, respectively. Five trials were conducted with the electric field activated at low, medium, and high settings and four trials were conducted with electric field off.

Logistic regression was used to determine if variability in the proportion of sea lampreys approaching the confluence each night was explained by electric field setting or the Ocqueoc River water temperature. Sea lampreys that approached the confluence were assigned to one of four categories based on their initial movement pattern at the confluence: (1) moved upstream of the confluence either in Silver Creek or the Ocqueoc River, (2) captured in trap, (3) did not move upstream of the confluence, but reversed migration after approaching the confluence, or (4) did not move upstream of the confluence, but settled upstream of the PIT tag antenna downstream of the confluence. To determine if the fate of sea lampreys that approached the confluence (four categories above) differed significantly among electric field treatments, mixed effect logistic regression models were used where the fixed effect was electric field setting and the random effect was trial date.

Visual observation of sea lamprey movements occurred at two locations; 14 m downstream of the trap to 4 m downstream of the trap (2–12 m transects on stream grid) and from 4 m downstream of the trap to the trap funnel (12–16 m transects on the stream grid). Sea lamprey movement tracks were recorded as described in Silver Creek trapping methods (Section 2.4.2). Observed sea lampreys were assigned to one of three categories based on their movement pattern: (1) moved directly toward the trap, (2) moved into the electric field, or (3) moved downstream without encountering the electric field. Furthermore, sea lampreys that entered the electric field were assigned to one of five categories based on their response: (1) deflected toward the trap defined as a net upstream movement toward the trap, (2) moved downstream defined as a net downstream movement away from trap, (3) escaped through the electric field defined as passing upstream of the second line of positive electrodes, (4) stunned defined as paralysis lasting less than 2 s or a sharp, quick movement, or (5) paralyzed defined as a lack of movement for more than 2 s. Sea lampreys observed moving within 1 m of the trap funnel were assigned to one of four categories: (1) moved into the funnel and entered the trap, (2) moved into the funnel but did not enter trap, (3) moved downstream away from the funnel, or (4) moved into the electric field. Logistic regression was used to determine if the fate of sea lampreys as assigned to the categories listed above differed significantly among electric field settings.

2.5. Methods to test prediction 3: A VE-PDC field will modify behavior of non-target species, but not injure or kill them after acute exposure

2.5.1. Rainbow trout and white sucker blocking and trapping experiments

The ability of VE-PDC fields to block and guide rainbow trout (*Oncorhynchus mykiss*) and white sucker (*Catostomus commersoni*) were tested because they migrate sympatrically with sea lamprey. Methods described for laboratory experiments to block and guide sea lampreys were used (Supplementary Methods). Rainbow trout were exposed to the VE-PDC field in the same laboratory raceway that yielded 100% blockage of sea lamprey and to the electric field that produced the highest capture rate of sea lamprey (Supplementary Results). Five trials were conducted for each treatment between 20 June 2011 and 24 June 2011.

2.5.2. Sea lamprey, rainbow trout, and white sucker electric field acute exposure experiments

Sea lamprey, rainbow trout, and white sucker were passed through the VE-PDC fields used for trapping experiments in the Ocqueoc River at medium and high settings (Fig. S6B and S6C) to determine rates of injury or mortality. As a control, the fish were also passed through the electric field when it was off. Fifty rainbow trout (average length = 341 mm, SD = 35; average weight = 411 g, SD = 110) were obtained from Harrietta Hills, LLC (Harrietta, MI) and 50 white suckers (average length = 152 mm SD = 15; average weight = 34 g SD = 11) were obtained from Michigan Wholesale Bait and Fish Farm (Alanson, MI). Sea lamprey, rainbow trout, and white sucker were held at HBBS for at least 7 days prior to experimentation in tanks supplied with Lake Huron water at ambient temperatures, which ranged from 7 to 14 °C. Two days before exposing the fish to the electric field, tank water temperatures were increased to 18 °C over the course of 24 h to match the Ocqueoc River temperature. Fish were stocked in acclamation cages (1 m^3) in the Ocqueoc River 20 h prior to experimentation. Rainbow trout were held in 3 cages (1 m^3) with 15 trout in each. White sucker and sea lamprey were held in one cage per species of the same dimensions as those used for rainbow trout.

To simulate the passage of downstream migrating fish through the VE-PDC field, one of each fish species was placed in a live net containing no metal (30 cm, 91 cm, 0.6 cm, Aquatic Sampling Gear, Buffalo, New York) and the live net was moved downstream through the electric field (between Q and R on the stream grid; Fig. 1). The live net was in the electric field for an average of 5 s (range = 4–6 s). Fifteen individuals of each species were subjected to each electric field setting (off, medium, high) except that only 11 sea lampreys were exposed to the high setting because four sea lampreys died while acclimating in the Ocqueoc River. The experiment took place on 25 July 2012 from 0840 to 1150 h and during the experiment, the Ocqueoc River water temperature was 16.4 °C and the ambient conductivity was 362 μS cm^{-1}.

After passage through the electric field, and a 1 h recovery period in the acclimation cages, fish were transported to HBBS in aerated tanks. Upon arrival at HBBS, the fish were placed in tanks according to species and treatment. Fish health was monitored for seven days after exposure. Specifically, the fish were visually inspected for mortality, noticeable hemorrhaging, discoloration, and inhibited swimming twice a day for one week according to Swink (1999). If mortality occurred during the 7-day monitoring period, the fish was measured, weighed, and dissected. Seven days after treatment, all remaining fish were euthanized with an overdose of tricaine methanesulfonate (Argent Laboratories, Redmond, Washington), measured, weighed, and dissected to determine the presence of musculature bruising and internal hemorrhaging. Bruising was defined as dark spots on the scales or flesh. Hemorrhaging was defined by spots with open wounds and blood.

To determine if the number of days fish survived after exposure to the VE-PCD field (longevity) within a species differed among electric field settings, a general linear model was used where longevity was square-root transformed to meet model assumptions of residual homoscedasticity. Logistic regression was used to determine if the proportion of fish exhibiting bruising, hemorrhaging, or scarring differed among treatments. Logistic regression models showed no evidence of overdispersion and no significant nonlinearities were observed when evaluated with generalized additive models with cubic splines.

3. Results

3.1. Prediction 1: A VE-PDC field will block sea lamprey migration

3.1.1. Sea lamprey migration was blocked by a VE-PDC field in a laboratory raceway

A VE-PDC field blocked 100% of sea lamprey movement in a raceway when generating a maximum voltage gradient of 1.8 V cm^{-1} between the line of positive and negative electrodes (90 V applied to electrodes; dual frequency; Supplemental Results, Tables S1 and S3). Electric field settings generating lower voltage gradients in the raceway or with longer intervals between pulses were less effective at blocking sea lamprey. For example, sea lamprey movement was not hindered by an electric field setting producing a voltage gradient of 0.3 V cm^{-1} halfway between positive and negative electrodes (45 V applied to electrodes).

3.1.2. Sea lamprey migration was blocked by a VE-PDC field in a natural stream

A VE-PDC field altered large-scale movement patterns of sea lampreys arriving at the confluence of Silver Creek and the Ocqueoc River (Table 1; Supplemental Results). When the electric field was installed across Silver Creek, no sea lamprey ascended Silver Creek and given the number of sea lampreys approaching the confluence during those trials ($n = 146$), the estimated escapement rate upstream of the Silver Creek electric field ranged from 0.0 to 2.5% (95% CI). When the electric field was installed across the Ocqueoc River, no sea lamprey ascended the Ocqueoc River and given the number of sea lampreys that approached the barrier ($n = 171$), the estimated escapement rate upstream of the Ocqueoc River electric field ranged from 0.0 to 2.1% (95% CI). When Silver Creek and the Ocqueoc River electric fields were both activated, two sea lampreys moved upstream of the Silver Creek electric field and the estimated escapement rates upstream of Silver Creek ranged from 0.0 to 3.3% (95% CI), and one sea lamprey moved upstream of the Ocqueoc River electric field and estimated escapement rates upstream of the Ocqueoc River electric field ranged from 0.0 to 2.5% (95% CI). When the Ocqueoc River was blocked or when both Silver Creek and the Ocqueoc River were blocked, sea lamprey were more likely to settle near the confluence (Ocqueoc block – $t_{874} = 4.517$; $P < 0.001$; both block – $t_{874} = 7.878$; $P < 0.001$) or reverse migration (Ocqueoc block – $t_{874} = 3.833$; $P < 0.001$; both block – $t_{874} = 3.261$; $P = 0.001$) than when the electric field was off (Table 1). When Silver Creek was blocked, sea lamprey were equally likely to reverse course, but less likely to settle near the confluence when compared to trials when the electric field was off (Table 1; reverse course – $t_{874} = -0.035$; $P = 0.972$; settle – $t_{874} = -2.703$; $P = 0.007$).

3.2. Prediction 2: A VE-PDC field will guide sea lamprey into a trap

3.2.1. Sea lamprey were directed to trap by a VE-PDC field in laboratory raceway

A VE-PDC field deflected sea lampreys toward a trap and reduced sea lamprey escapement upstream of a trap in a raceway. Compared to when the electric field was off, sea lamprey deflection rates toward the trap were significantly higher at all electric field settings tested and escapement upstream of the trap was significantly lower (Tables S2 and S4; deflection for all comparisons with control – $t_{427} < 2.04$; $P < 0.041$; escapement for all comparisons with control – $t_{427} < -4.6$; $P < 0.001$). However, sea lamprey capture rates were not significantly higher at any electric field setting tested. For example, the best trapping setting yielded a 15% capture rate, which was higher than when the electric field was off (10%), but the difference was not significant ($t_{1411} = 1.358$; $P = 0.18$; Table S4).

3.2.2. Sea lamprey were directed to a trap by a VE-PDC field in Silver Creek

Sea lampreys that approached the confluence were more likely to enter Silver Creek and be captured in the trap when the VE-PDC fields were on (Table 2; Supplemental Results). When the electric fields were on, 138 sea lampreys were observed swimming in Silver Creek and movements were concentrated below the electric field and near the trap (Fig. 2). Of those observed entering the electric field in Silver Creek, 42 sea lampreys were stunned, 20 were paralyzed, and 33 were deflected to the trap. Twenty-five sea lampreys were observed to enter the trap funnel but were not trapped and 18 entered the funnel and were trapped. The estimated trapping efficiency of sea lamprey that approached the confluence was

Table 1
A vertical electrode pulsed direct current field blocked sea lamprey migration in a natural stream. Number of pre-ovulatory female sea lampreys released (Released) and the percent of sea lampreys released that approached the confluence (Approach) when the pulsed DC electric field was off, blocked Silver Creek, blocked the Ocqueoc River, and blocked both Silver Creek and the Ocqueoc River. "Up Ocqueoc" is the percentage of sea lampreys that approached the confluence that passed upstream of the electric field in the Ocqueoc River, "Up Silver" is the percent of sea lampreys that approached the confluence that passed upstream of the electric field in Silver Creek, "Reverse" is the percent of sea lampreys that approached the confluence that reversed migration and moved back downstream, and "Settle" is the percent of sea lampreys that approached the confluence and did not move upstream in Silver Creek or the Ocqueoc River or reverse migration. Treatments with the same letter are not significantly different ($\alpha = 0.05$) as determined by mixed effect logistic regression.

Treatment	Released	Approach	Up Ocqueoc	Up Silver	Reverse	Settle
Off	239	88% a	65% a	20% a	6% a	9% a
Block Silver	200	73% b	92% a	0% b	7% a	1% b
Block Ocqueoc	199	86% a	0% c	24% a	31% b	45% c
Block Both	240	91% a	0% c	1% b	23% b	76% d

Table 2
A vertical electrode pulsed direct current field directed sea lampreys from a large stream to a small stream and into a trap within that small stream. The number of pre-ovulatory female sea lampreys released (Released) and the percent of sea lampreys released that approached the confluence (Approach) when the electric fields were off and on. "Up Ocqueoc" is the percentage of sea lampreys that approached the confluence that passed upstream of the electric field in the Ocqueoc River. "Obs in Silver" is the number of sea lampreys that were visually observed entering Silver Creek. "Up Silver" is the percent of sea lampreys that approached the confluence that passed upstream of the electric field in Silver Creek. "Trap" is the percent of sea lampreys that approached the confluence that were captured in the fyke net. "Reverse" is the percent of sea lampreys that approached the confluence that reversed migration and moved back downstream. "Settle" is the percent of sea lampreys that approached the confluence and did not move upstream in Silver Creek or the Ocqueoc River or reverse migration. Treatments with the same letter are not significantly different ($\alpha = 0.05$) as determined by mixed effect logistic regression (percent metrics) and general linear model (Obs in Silver).

Treatment	Released	Approach	Up Ocqueoc	Obs in Silver	Up Silver	Trap	Reverse	Settle
OFF	160	84% a	95% a	3 a	1% a	0% a	3% a	1% a
ON	199	89% a	13% b	138 b	1% a	10% b	21% b	55% b

between 6.1 and 15.6% when the electric field was on and 0.0–2.7% (95% CI) when off. When the electric fields were off, three sea lampreys were observed in Silver Creek, which was significantly less than when the electric fields were on ($F_{[1,7]} = 312$; $P < 0.001$). Sea lamprey were more likely to reverse migration or settle near the confluence when the electric field was on (reverse – $t_{355} = 3.096$; $P = 0.002$; settle – $t_{355} = 6.015$; $P < 0.001$).

3.2.3. *Sea lamprey were directed to a trap by a VE-PDC field in the Ocqueoc River*

Sea lampreys that approached the confluence were more likely to be captured when the VE-PDC field was on (Table 3; Supplemental Results). Trapping efficiency at the medium setting (33%) was significantly higher than the trapping efficiency at the high setting (24%; $t_{768} = 2.00$; $P = 0.045$), but was not significantly higher than the trapping efficiency of sea lamprey at the low setting (25%; $t_{768} = 1.718$; $P = 0.086$). Sea lamprey were more likely to escape upstream of the trap when the electric field was off than at all other electric field settings (all comparisons $t_{768} > 3.503$; $P < 0.001$). Escapement rate upstream of the electric field was significantly higher at the low electric field setting than at the medium or high electric field setting (medium – $t_{768} = -2.053$; $P = 0.040$; high – $t_{768} = -2.719$; $P < 0.007$). Sea lamprey were more likely to reverse course when the electric field was on (all comparisons; $t_{768} > 2.533$; $P < 0.011$), but reversals did not differ significantly among the different settings (low vs. medium – $t_{768} = 1.551$; $P = 0.121$; low vs. high – $t_{768} = 0.128$; $P = 0.898$; medium vs. high – $t_{768} = -1.473$; $P = 0.141$). Sea lamprey were more likely to settle downstream of the trap when the electric field was on (all comparisons – $t_{768} > 4.765$; $P < 0.001$).

More sea lampreys were observed when the electric field was on than when it was off (Fig. 3). The primary movement pattern for sea lamprey during all treatments was to swim upstream into the electric field (Table S5). Differences in sea lamprey behavior were observed after they entered the electric field where downstream movements, stuns, and paralysis were higher when the electric field was on and escapements upstream of the electric field were higher when it was off (Table S6). During low setting trials, sea lamprey within 1 m of the trap were more likely to be trapped than when the electric field was off (Table S7; $t_{261} = 2.006$; $P = 0.045$), but during medium and high setting trials no difference was observed.

3.3. *Prediction 3: A VE-PDC field will modify behavior of non-target species, but not injure or kill them after acute exposure*

3.3.1. *Non-target behavior was modified by a VE-PDC field in laboratory raceway*

The VE-PDC field that blocked 100% of sea lamprey in a raceway (Table S3) also blocked 100% of rainbow trout, but rarely were rainbow trout shocked or paralyzed by the electric field (Table S8). Typically, rainbow trout only challenged the electric field once and avoided being stunned or paralyzed by promptly moving downstream when the electric field was encountered. No rainbow trout where injured or killed when attempting to pass through the electric field.

The VE-PDC field that produced the highest capture rate of sea lamprey in the raceway (Table S4) did not change the trap capture rate of rainbow trout (off capture rate = 1.5%; on capture rate = 3.5%; $t_{178} = 0.778$; $P = 0.436$) or white sucker (off capture rate = 40%; on capture rate = 20%; $t_{47} = -1.42$; $p = 0.157$; Table S9). Rainbow trout and white sucker were less likely to move upstream of the trap when the electric field was on (Table S9).

3.3.2. *Sea lamprey, rainbow trout, and white sucker had minimal injuries after acute exposure to a VE-PDC field*

Minimal differences in longevity, hemorrhaging, or scarring was observed in fish exposed to the VE-PDC field when it was off, at medium, or high settings (Table S10 and herein). White sucker had significantly higher rates of bruising when exposed to the high electric field setting than when off or at medium setting ($t_{40} = 1.96$; $P = 0.05$) and longer fish were more likely to be bruised ($t_{40} = 2.28$; $P = 0.023$). In no other cases did the explanatory variables of treatment, length, or weight explain significant variability in longevity, bruising, hemorrhaging, or scarring. An anecdotal observation from this study was that several raccoons (*Procyon lotor*) and beavers (*Castor canadensis*) interacted with the electric field with little apparent discomfort or injury.

Table 3
A vertical electrode pulsed direct current field directed sea lampreys in a large stream into a trap. The number of pre-ovulatory female sea lampreys released (Released) and the percent of the sea lampreys released that approached the confluence (Approach) when the electric field was off and when the electric field was activated as a non-physical lead at low, medium, and high intensity to guide sea lampreys to a fyke net in the Ocqueoc River. "Trap" is the percentage of sea lampreys that approached the confluence that were captured in the trap, "Past" is percentage of sea lampreys that approached the confluence and moved upstream of the trap, "Reverse" is the percent of sea lampreys that approached the confluence that reversed migration and moved back downstream, and "Settle" is the percent of sea lampreys that approached the confluence and did not move upstream of the trap or reverse migration. Treatments with the same letter are not significantly different ($\alpha = 0.05$) as determined by mixed effect logistic regression.

Treatment	Released	Approach	Trap	Past	Reverse	Settle
OFF	200	72% a	4% a	92% a	2% a	2% a
Low	178	64% a	25% bc	24% b	11% b	40% b
Medium	198	71% a	33% c	5% c	16% b	46% b
High	197	60% b	24% b	1% c	13% b	62% c

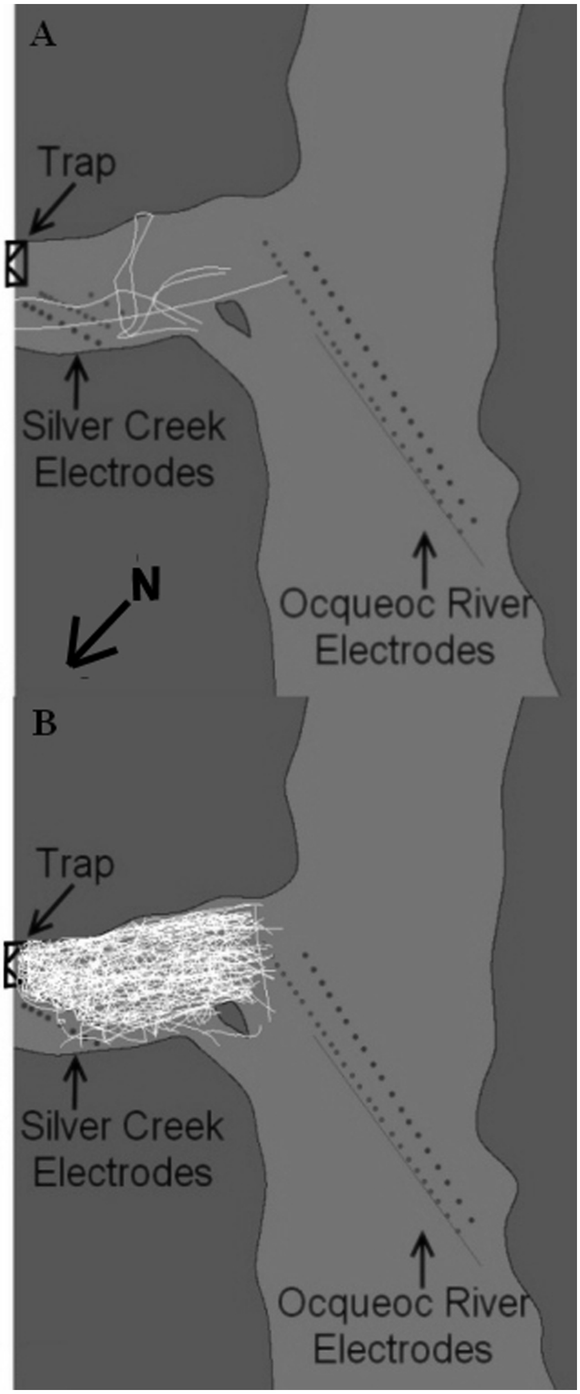

Fig. 2. Visually observed movement tracks of sea lampreys in Silver Creek when vertical electrode pulsed direct current fields were not activated (A) and activated (B). Light lines in the river are observed sea lamprey movement tracks. Light dots are the positions of positive electrodes. Dark dots are the positions of negative electrodes. The dark line near positive electrodes is the position of a steel cable placed on the stream bottom that served as a positive electrode.

4. Discussion

4.1. Prediction 1: VE-PDC fields will block sea lamprey migration

Our first prediction was supported when adult sea lamprey migration was blocked in a raceway and in natural streams. In a raceway, 100% of sea lamprey movement was blocked by a VE-PDC field with an average power density of 0.3 mW/cm^3 (between the positive and negative electrodes) whereas in Silver Creek or the Ocqueoc River, a power density greater than 4.4 mW/cm^3 was required to block sea lamprey migration. Discrepancies between lab and field results are not unheard of (i.e. Riley et al., 2005) and have been observed in sea lamprey chemosensory research (Johnson and Li, 2010). Here the discrepancy in the power density needed to block sea lamprey in the lab and field was likely attributed to the confined nature of the raceway and differences in water temperature and chemistry (Lake Huron water versus Ocqueoc River water) and emphasizes why laboratory results should be confirmed in the field.

Complete blockage of invasive fish with high reproductive potential must occur to stop the invasion front. Electric barriers and guidance systems have been used to block sea lamprey, but most applications were decommissioned because few blocked 100% of sea lamprey passage, presumably because of periodic floods, power outages, or equipment failure (McLain et al., 1965; Lavis et al., 2003; Clarkson, 2004). Two permanent installations of horizontal electrode PDC barriers (Swink, 1999 describes one of them) were also decommissioned because they did not block 100% of sea lamprey and limited migration of non-target species (Personal communication Jessica Barber, USFWS).

Concluding that 100% blockage of a natural run of sea lamprey can be achieved over the entire migratory period with VE-PDC is premature. When only Silver Creek or the Ocqueoc River was electrified, 100% blockage of sea lamprey migration was achieved, but when both Silver Creek and the Ocqueoc River were electrified, one sea lamprey escaped upstream of the Ocqueoc River barrier and two sea lampreys escaped upstream of the Silver Creek barrier. Although few lampreys were observed passing the barriers in this study, escapement rates may be conservative because sea lampreys were only monitored for one night after release. A natural run of sea lamprey would have more opportunity to escape above the barrier. Management-scale experiments over the course of the spawning migration are needed to confirm that complete blockage can be achieved. These results suggest that power densities greater than 4.4 mW/cm^3 would be required to achieve complete blockage of a natural run of sea lampreys.

Use of VE-PDC to block sea lamprey migration could reduce the amount of selective pesticide applied to Great Lakes tributaries if 100% blockage is realized. Spawning habitat available to adult sea lamprey is limited by existing dams and purpose built low-head barriers (Hunn and Youngs, 1980; Jones et al., 2003; Lavis et al., 2003). Some existing dams that block sea lamprey migration have deteriorated, allow sea lamprey passage, and now require lampricide treatment (McLaughlin et al., 2012). At structures that no longer block sea lamprey migration, VE-PDC could be quickly and temporarily installed to block sea lamprey migration until repairs occur. Another option is to use VE-PDC in streams that are costly to treat with pesticides, difficult to access, or have consistently low treatment effectiveness. In these streams, VE-PDC could be operated without conventional power and would not produce an undesirable rise in stream levels like low-head barriers.

4.2. Prediction 2: A VE-PDC field will guide sea lamprey into a trap

Our second prediction was supported when adult sea lamprey were more likely to enter freestanding traps when a VE-PDC field was used as a non-physical lead. Trap efficiency increased from 0 to 10% in Silver Creek and from 2 to 33% in the Ocqueoc River (medium setting) when the electric trap lead was activated. Traps with electric leads captured more sea lampreys because the probability of trap encounter increased, not because the probability of trap entry after encounter increased. In raceway and in-stream experiments, sea lampreys were less likely to pass upstream of the trap when the electric leads were activated. Sea lampreys that encountered an

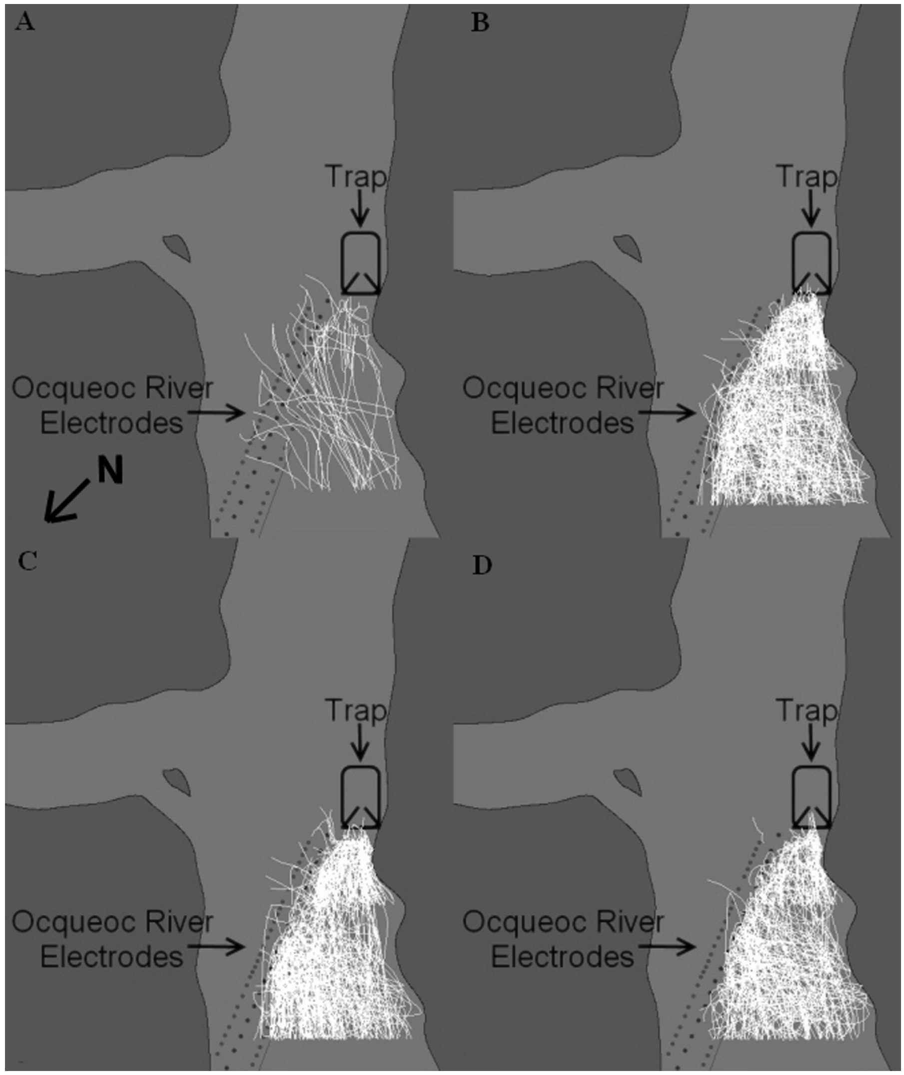

Fig. 3. Visually observed movement tracks of sea lampreys in the Ocqueoc River when the vertical electrode pulsed direct current field was not activated (A) and activated at low (B), medium (C), and high (D) settings. Light lines are observed sea lamprey movement tracks. Light dots are the positions of positive electrodes. Dark dots are the positions of negative electrodes. The dark line near the positive electrodes is the position of a steel cable placed on the stream bottom that served as a positive electrode.

electric lead moved downstream or were deflected toward the trap. Observations during raceway experiments and movement tracks of individual sea lamprey showed that sea lampreys blocked by the electric lead encountered the electric lead and the trap multiple times. In most cases, capture rates of sea lampreys encountering the trap did not differ significantly whether the electric field was on or off. Only about 45% of the sea lampreys that entered the trap funnel during the Ocqueoc River trapping experiments were captured in the trap, showing that trap funnel design could be further improved.

Trapping invasive fish reduces reproductive potential and allows for population assessment. At present, sea lamprey trapping is only effective at physical barriers to sea lamprey migration, where individuals repeatedly encounter traps as they search for routes past the barrier. In 2011, barrier-integrated traps had an average efficiency of 37% (SD = 22) and were fished in 10% of sea lamprey producing streams (Sullivan and Adair, 2012). Most untrapped streams could not be efficiently trapped with current technology because they lack a natural or manmade sea lamprey barrier. Sea lamprey control and assessment may be further improved if VE-PDC can be used to lead lampreys into traps. In remote streams without available power, VE-PDC could be deployed as trap leads and powered by batteries or small generators. Given the portable nature of vertical electrodes, a single system could be used on different streams from year to year. Taken together, this technology could enable sea lamprey trapping on streams which were previously not able to be trapped, thereby advancing trapping for control (Great Lakes Fishery Commission, 2011) and improving adult assessment (Mullett et al., 2003).

4.3. Prediction 3: A VE-PDC field will modify behavior of non-target species, but not injure or kill them after acute exposure

Our third prediction was supported when rainbow trout and white sucker avoided VE-PDC, but were not injured after acute exposure. Sea lamprey had a higher tolerance for VE-PDC compared to rainbow trout and white sucker. Sea lamprey proceeded upstream into the electric field until they were stunned or paralyzed, whereas rainbow trout and white sucker generally moved downstream before being stunned or paralyzed. To reduce impacts of VE-PDC trap leads on non-target fish passage, leads might only be activated at night when sea lampreys migrate; as was done by Klingler (1997) to allow rainbow trout passage. Alternatively, the difference in behavior between sea lamprey and non-target species may be exploited by using a weak electric field to deflect non-target species away from traps, whereas sea lamprey would ignore the electric field and move upstream into traps. Given the results of non-target behavior experiments and previous studies (Verrill and Berry, 1995; Savino et al., 2001; Dawson et al., 2006), VE-PDC may also be effective at blocking or guiding other invasive fishes such as rainbow trout, carps (family *Cyprinidae*), and northern pike (*Esox lucius*). Such a system may also be useful to guide valued fishes away from hydropower facilities or to enhance assessment (Palmisano and Burger, 1988).

Injury rates of rainbow trout, white sucker, and sea lamprey after acute exposure to the VE-PDC field was low. Shorter longevity of sea lamprey and white sucker under all settings was likely attributed to sea lamprey being in their terminal life stage and white sucker contracting a fungal infection. In a similar, but more comprehensive study, white sturgeon (*Acipenser transmontanus*) avoided a PDC electric sea lion barrier with maximum voltage gradients of 2.5 V cm^{-1} with a 0.4 ms pulse width at 2 Hz. After acute exposure to the electric field white sturgeon had negligible cell or tissue damage, but when a white sturgeon was entrained in an electric field in a state of narcosis, mortality occurred (Ostrand et al., 2009). The likelihood of chronic electroshock can be reduced by placing barriers in areas with high water velocity so narcosed fish are swept downstream out of the electric field. The impact of human exposure to PDC electric fields has not been investigated, but to date no human injuries or deaths have been associated with electric fish barriers (personal communication, Carl Burger, Smith-Root).

4.4. Comparison of vertical and horizontal electrode PDC

The primary difference between VE-PDC and horizontal electrode PDC (HE-PDC) fields is the plane in which the electric field intensity varies (Reynolds and Kolz, 2012). HE-PDC fields vary on the vertical plane and the electric field is most intense near the substrate (electrodes) and decreases in intensity near the surface of the water. VE-PDC fields vary on the horizontal plane where the electric field intensity decreases as horizontal distance from the electrode increases. Comparisons of the VE-PDC field used in this study to previous studies using HE-PDC fields are difficult because waveforms and pulse characteristics vary and electric field parameters were not reported in all studies. For reference, an AC electric barrier with a power density of 1.2 mW/cm^3 blocked sea lamprey migration in the Ocqueoc River (Applegate et al., 1952). The voltage gradient or power density produced by HE-PDC used to block sea lamprey (Swink, 1999; pulse width 1 ms at 10 Hz), common carp, and bigmouth buffalo (Verrill and Berry, 1995; pulse characteristics not reported) were not reported. Round goby were blocked by a DC barrier with power density of 24.7 mW/cm^3 and pulse width of 5 ms at 2 Hz (Savino et al., 2001), while Eurasian ruffe were more likely to pass through the same electric field than were round goby (Savino et al., 2001; Dawson et al., 2006).

A practical advantage of vertical electrodes is that they can be installed quickly and without major stream modification. A practical disadvantage of vertical electrodes is that unlike horizontal electrodes, which are flush with the stream bottom, vertical electrodes are suspended in the water column and exposed to stream debris. Vertical electrodes can be hung from overhead cables (this study) or anchored to the bottom using surface or subsurface floats to keep them vertical. Applegate et al. (1952) used vertical electrodes mounted from overhead lines to produce AC electric barriers and concluded that the suspended electrode system was satisfactory and was not damaged or displaced by floating debris. In the current study, electrodes were not prone to electroplating, did not require cleaning, and were not dislodged by woody debris, but experimental streams were small (width less than 20 m) and significant flood events were also not experienced. Advances in engineering and material sciences make it likely that self-cleaning vertical electrodes can be designed and can provide low cost, low impact solutions for aquatic invasive species control and fish guidance at dams. However, long term in-stream experiments are still needed to determine if improved engineering solutions for mounting vertical electrodes can withstand high flow events.

4.5. Conclusions

Our hypothesis that sea lamprey would exhibit behavioral avoidance to a VE-PDC field and that the electric field would not injure or kill sea lamprey or non-target fish was supported by all three predictions. Long term in-stream experiments are needed to determine (1) if complete blockage of sea lamprey migration can be achieved to eliminate the need for selective pesticide treatments, (2) if freestanding traps with VE-PDC leads can yield sufficient trapping efficiencies to obtain population estimates and reduce recruitment, and (3) if vertical electrodes can be engineered to self-clean and withstand floods in rivers larger than the ones used in this study. Use of VE-PDC for blocking or trapping other invasive species may also prove useful for slowing the invasion front. Similar VE-PDC fields may be advantageous for improving fish passage at dams and warrants further investigation. For example, the same VE-PDC guidance system tested here was recently shown to guide the out-migration of juvenile sea lamprey (up to 84% success rate) and may be useful for reducing entrainment at hydropower facilities in their native range where populations are threatened (Johnson and Miehls, 2013).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2013.10.006.

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Blocking and Guiding Adult Sea Lamprey with Pulsed Direct Current from Vertical Electrodes

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Content description: Detailed methods and results of laboratory and in-stream experiments to block and guide sea lamprey, rainbow trout, and white sucker in experimental raceways are provided.

S1. Supplementary Methods

S1.1. Test subjects for laboratory experiments

S1.1.1. Sea lamprey

Adult female sea lamprey (*Petromyzon marinus*) were captured in mechanical traps operated in tributaries to northern Lake Michigan and Lake Huron by agents of the United States Fish and Wildlife Service (USFWS) and the Department of Fisheries and Oceans, Canada, from May through June, 2011. Females were identified by their soft abdomen and were separated from males which were identified by their dorsal ridge (Vladykov, 1949). Further, females were identified as pre-ovulatory if eggs were not expressed with manual pressure to the abdomen.

Three hundred and fifty pre-ovulatory females were stored at United States Geological Survey, Hammond Bay Biological Station (HBBS) in a 1,000 L flow-through tank supplied with water from Lake Huron at ambient temperatures which ranged from 7 to 14° C. This group of female sea lamprey was used in laboratory bioassays to determine if vertical electrode pulsed direct current (hereafter, VE-PDC field) can block sea lamprey migration and guide them to traps. Use of the HBBS raceway was limited to 0700 to 1500 h daily because of use by another research group. Because sea lamprey migrate at night (Applegate, 1950), sea lampreys experimented on in the raceway were photo-reversed by subjecting them to a 14L:10D photoperiod where darkness occurred from 0700 to 1700 h. Ambient light was blocked from entering the tank using black plastic sheeting. Experimental subjects were given a minimum of three days to acclimate to the change in their photoperiod. The three day photoreversal period was considered adequate based on a laboratory study by Kleerekoper et al. (1961) who found that photoperiod can be re-established in sea lamprey after exposing the experimental animals to 1-2 artificial diurnal light cycles.

S1.1.2. Rainbow trout

One hundred rainbow trout (*Oncorhynchus mykiss*) ranging from 25 to 36 cm in total length were obtained from Harrietta Hills, LLC (Harrietta, Michigan) and were stored in a 1,000 L flow-through tank supplied with water from Lake Huron at ambient temperatures which ranged from 10 to 14° C at HBBS. No feed was administered to rainbow trout because they were only in holding at HBBS for two days prior to experimentation.

S1.1.3. White sucker

One hundred white sucker (*Catosomus commersonii*) ranging from 15 to 20 cm in total length were obtained from Michigan Wholesale Bait and Fish Farms (Alanson, Michigan) and were stored in a 1,000 L flow-through tank supplied with water from Lake Huron at ambient temperatures which ranged from 10 to 14° C at HBBS. No feed was administered to white suckers because they were only in holding at HBBS for two days prior to experimentation.

S1.2. Experimental raceway

Bioassays were conducted in a darkened indoor laboratory raceway at HBBS between 0800 and 1400 h. During experimentation, visible light was blocked from entering the raceway room by covering windows and doors with black plastic sheeting. The raceway received a continuous discharge of 680 $L \cdot min^{-1}$ of Lake Huron water at ambient temperatures which ranged from 7 to 14° C and had a conductivity of 90 $\mu s \cdot cm^{-1}$ during experimentation. The depth of the raceway was held at 20 cm resulting in a water velocity in the raceway ranging from 5 to 8 $cm \cdot s^{-1}$. A 5.00 x 1.85 m section of the raceway was illuminated with infrared lights and fish behavior within the above mentioned section was recorded with an overhead night-vision video camera.

S1.3. Laboratory experiment to determine if a VE-PDC field blocks sea lamprey migration

The electric field was arrayed at right angles of the longitudinal center of the raceway observation area (Fig. S1). Six female sea lampreys were acclimated in a holding cage at the downstream end of the raceway for at least 2 h prior to experimentation. At the beginning of each trial, the 6 sea lampreys were released at the downstream end of the raceway. Released sea lampreys were allowed to search the raceway for 20 min, then were removed from the raceway and never used again. The following occurrences were recorded during the 20 min experimental period: the number of times sea lampreys 1) entered the electric field defined as the location with greater than 0.1 V cm^{-1} and as illustrated in Fig. S1, 2) moved upstream of the electric field, defined as upstream of the negative electrodes, 3) were stunned, defined as paralysis lasting less than 2 s or a sharp, quick movement, and 4) paralyzed, as defined as an inability to move for more than 2 s.

Five electric settings with different field strength and pulse characteristics were tested (Table S1). The electric field was turned off as the negative control. Five trials were conducted for each setting. Experiments were conducted between 07 June 2011 and 12 June 2011. Significant differences in the proportion of sea lampreys which entered the electric field and then also 1) moved upstream of the electric field, 2) were stunned, or 3) paralyzed were determined with a logistic regression model where variability in the response variable was explained by electric setting. Logistic regression models showed no evidence of overdispersion or heterostedasticity. All statistical tests reported were conducted in R Version 2.9.2 (R Development Core Team, 2009).

S1.4. Laboratory experiments to determine if VE-PDC field can direct migrating sea lampreys toward a trap

The electric field was arrayed at a 30 or 45º angle across the raceway as a lead to a USFWS standard aluminum sea lamprey portable assessment trap (0.359 m^3; Fig. S2). Experimental animals were acclimated, released, and monitored as described in laboratory experiments to block sea lamprey (S1.3.). The number of times sea lampreys moved upstream of the release area, the number of times sea lampreys were stunned and paralyzed by the electric field, and the percentage of sea lampreys of which entered the electric field that were deflected toward the trap or passed upstream of the electric field was recorded. The total number of sea lampreys captured in the trap was also recorded. Deflection and passage rates were calculated by dividing the number of times sea lamprey were deflected toward the trap or moved upstream of the electric field by the number of times sea lamprey moved in the electric field, which was then multiplied by 100. Capture rate was calculated by dividing the number of sea lampreys captured by the number of times sea lampreys moved upstream, which was then multiplied by 100.

Eight settings with different field strength and pulse characteristics were tested (Table S2). The electric field was turned off as the negative control. Three to nine trials were conducted for each electric setting. Experiments were conducted between 13 June 2011 and 22

June 2011. Significant differences in 1) deflection rate, 2) passage rate, and 3) capture rate among settings was determined with a logistic regression model where variability in the response variable was explained by the setting.

S2. Supplementary Results

S2.1. Prediction 1: A VE-PDC field will block sea lamprey migration

S2.1.1. Sea lamprey migration was blocked by a VE-PDC field in spawning tributaries

Upstream migration of sea lamprey to the confluence of Silver Creek and the Ocqueoc River was positively correlated with Ocqueoc River water temperature at the time of release ($t_{873} = 2.07$, $P = 0.040$). The proportion of sea lampreys moving upstream to the confluence of Silver Creek and the Ocqueoc River when Silver Creek electric field was activated was significantly lower than when the electric field was off (Table 1). Therefore, fewer sea lampreys approached the confluence during Silver Creek blocking trials because those trials were randomly conducted on nights when the Ocqueoc River temperature was lower than average.

S2.2. Prediction 2: A VE-PDC field will guide sea lamprey into a trap

S2.2.1. Sea lamprey were directed to trap by a VE-PDC in Silver Creek

Upstream migration of sea lamprey to the confluence of Silver Creek and the Ocqueoc River was positively correlated with Ocqueoc River water temperature at the time of release ($t_{358} = 3.49$, $P > 0.001$). The proportion of sea lampreys moving upstream to the confluence when the electric fields were activated versus not activated did not differ significantly (Table 2).

S2.2.2. Sea lamprey were directed to trap by a VE-PDC field in Ocqueoc River

Upstream migration of sea lamprey to the confluence of Silver Creek and the Ocqueoc River was positively correlated with Ocqueoc River water temperature at the time of release (t_{767}=6.05, P > 0.001). The proportion of sea lampreys moving upstream to the confluence of Silver Creek and the Ocqueoc River when electric field setting was high was significantly lower than when the electric field was off (Table 3). Therefore, fewer sea lampreys approached the confluence during trials when the electric field setting was high because those trials were randomly conducted on nights when the Ocqueoc River temperature was lower than average.

Supplementary References

Applegate, V.C., 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Fish and Wildlife Service Spec. Sci. Rep. Fish. 55, 237.

Kleerekoper H., Tayler G., Wilton R., 1961. Diurnal periodicity in the activity of *Petromyzon marinus* and the effects of chemical stimulation. Trans Am Fish Soc 90, 73-78.

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Supplementary Tables

Table S1

The vertical electrode pulsed direct current settings tested to block sea lamprey migration in a raceway. The electric field was set perpendicular to stream flow to block sea lamprey movement. The table lists voltage of direct current (DC) pulse, the maximum voltage gradient measured in the raceway, and the pulse settings. A pulse setting of 1.8, 8.2, 41.8, 200.0 means that there were five1.8 ms pulses with four 8.2 ms off-periods in between for a total duration of 41.8 ms per group of pulses. The duration from the start of one group to the next was 200 ms.

Setting	DC Pulse (V)	Max Voltage Gradient (V cm^{-1})	Pulse Settings (ms)
1	90 +/- 1	1.8	1.8, 8.2, 41.8, 200.0
2	90 +/- 1	1.8	1.8, 8.2, 41.8, 100.0
3	60 +/- 1	0.9	1.8, 8.2, 41.8, 100.0
4	60 +/- 1	0.9	1.8, 8.2, 41.8, 200.0
5	45 +/- 1	0.3	1.8, 8.2, 41.8, 200.0

Table S2
The vertical electrode pulsed direct current settings tested to guide sea lamprey into a trap in the raceway. The table lists voltage direct current (DC) pulse, the maximum voltage gradient measured in the raceway between positive and negative electrodes, and pulse settings. A pulse setting of 1.8, 8.2, 41.8, 200.0 means that there were five1.8 ms pulses with four 8.2 ms off-periods in between for a total duration of 41.8 ms per group of pulses. The duration from the start of one group to the next was 200 ms. Electrodes were set at a 30 or 45º angle from the trap when referencing flow direction. In some trials the trap was used as a negative electrode. The metal trap acted as a Faraday cage eliminating the electric field inside the trap when used as an electrode.

Setting	Angle(º)	DC Pulse (V)	Voltage Gradient (V cm^{-1})	Pulse Settings (ms)	Trap used as electrode?
1	45-50	45 +/-1	0.9	1.8, 8.2, 41.8, 200.0	No
2	45-50	60 +/-1	1.4	1.8, 8.2, 41.8, 200.0	No
3	45-50	60 +/-1	1.4	1.8, 8.2, 41.8, 200.0	Yes
4	45-50	45 +/-1	0.9	1.8, 8.2, 41.8, 200.0	Yes
5	45-50	45 +/-1	0.9	1.8, 8.2, 41.8, 150.0	Yes
6	45-50	45 +/-1	0.9	1.8, 8.2, 41.8, 100.0	Yes
7	30	45 +/-1	0.9	1.8, 8.2, 41.8, 100.0	Yes
8	30	60 +/- 1	1.4	1.8, 8.2, 41.8, 100.0	Yes

Table S3

Behavioral responses of adult sea lampreys to a vertical electrode pulsed direct current field in a raceway. The table lists the number of times sea lampreys moved into the electric field, passed upstream of the electric field and the number of times sea lampreys were stunned and paralyzed in the electric field. Within the "Electric field", "Upstream of field", "Stunned" and "Paralyzed" data fields, settings with the same letter were not significantly different at $\alpha = 0.05$ as determined by logistic regression (i.e. "Upstream of field" when OFF (A) is significantly different than "Upstream of field" at setting 1 (C)).

Setting	Trials	Electric field	Upstream of field	Stunned	Paralyzed
OFF	5	191 A	112 A	0 A	0 A
1	5	111 B	2 C	56 C	53 D
2	5	103 B	0 C	45 C	50 D
3	5	128 B	8 C	66 C	36 C
4	5	162 AB	64 B	88 C	10 B
5	5	172 AB	104 A	10 B	0 A

Table S4
Behavioral responses of adult sea lampreys to a vertical electrode pulsed direct current field arrayed as a non-physical trap lead. The table lists the number of times sea lampreys moved upstream of the release area, the number of times sea lampreys were stunned and paralyzed in the electric field, and the percentage of sea lampreys which entered the electric field that were deflected toward the trap or passed upstream of the electric field. The total number of sea lampreys captured in the trap is also reported. Within the "Deflection rate", "Passage rate", and "Capture rate" data fields, settings with the same letter were not significantly different at $\alpha = 0.05$ as determined by logistic regression.

Setting	Trials	Upstream	Stunned	Paralyzed	Deflection rate	Passage rate	Trapped (n)	Capture rate
OFF	9	225	0	0	3% A	86% A	23	10% A
1	5	197	37	6	19% BC	25% C	12	6% B
2	7	175	59	12	23% BCD	8% BC	10	6% B
3	5	97	37	20	36% CD	5% B	9	9% A
4	5	69	9	13	19% BC	3% B	9	13% A
5	3	47	15	5	32% CD	27%C	2	4% B
6	5	85	7	20	16% BC	7% BC	5	6% B
7	9	162	23	23	39% CD	20% C	24	15% A
8	5	93	16	30	39% CD	32% C	11	12% A

Table S5

Observed movement patterns of sea lampreys in the Ocqueoc River before entering the electric field. The number of sea lampreys observed (n) from 14 to 4 m downstream of the trap when the vertical pulsed DC non-physical lead was off, on low, medium, and high intensity. “Trap” is the percent of sea lampreys observed that moved directly to the trap without interacting with the electric field, “Electric Field” is the percent of sea lampreys observed that moved into the electric field, and “Downstream” is the percent of sea lampreys observed that moved downstream without interacting with the electric field. Treatments with the same letter are not significantly different (α=0.05) as determined by logistic regression.

Treatment	n	Trap	Electric Field	Downstream
OFF	34	15% a	82% a	3% a
Low	195	14% a	81% a	5% a
Medium	312	17% a	78% a	5% a
High	241	10% a	83% a	7% a

Table S6
Observed movement patterns of sea lampreys in the Ocqueoc River after entering the electric field. The number of sea lampreys observed (n) from 14 to 4 m downstream of the trap (Below Trap) and from 4 to 0 m downstream of the trap (Near Trap) when the vertical pulsed DC non-physical lead was off, on low, medium, and high setting. "Deflected" is the percent of sea lampreys observed that moved toward the trap after encountering the electric field, "Downstream" is the percent of sea lampreys observed that moved downstream after interacting with the electric field, "Stunned" is the percent of sea lampreys observed that were stunned in the electric field, "Paralyzed" is the percent of sea lampreys observed that were paralyzed in the electric field, and "Escape" is the percent of sea lampreys that escaped upstream of the electric field. Treatments with the same letter are not significantly different (α=0.05) as determined by logistic regression.

Treatment	Location	n	Deflected	Downstream	Stunned	Paralyzed	Escape
OFF	Below Trap	28	7% a	0% a	0% a	0% a	93% a
Low		158	14% a	44% b	20% b	13% b	9% b
Medium		243	10% a	36% bc	35% b	17% bc	3% bc
High		199	11% a	34% c	31% b	24% c	1% c
OFF	Near Trap	6	17% a	17% a	0% a	0% a	67% a
Low		54	24% a	24% a	22% b	22% b	7% b
Medium		50	28% a	18% a	16% b	36% b	2% b
High		50	28% a	16% a	12% b	44% b	0% c

Table S7
Observed movement patterns of sea lampreys in the Ocqueoc River within 1 m of the trap. The number of sea lampreys observed (n) moving within 1 m of the trap funnel when the electric field was off, on low, medium, and high intensity. "Trapped" is the percent of observed sea lampreys that entered the funnel and were captured, "Funnel" is the percent of observed sea lampreys that entered the trap funnel and were not captured, "Downstream" is the percent of sea lampreys that moved downstream without encountering the trap or the electric field, and "Electric Field" is the percent of sea lampreys that did not enter the trap funnel and moved into the electric field. Treatments with the same letter are not significantly different (α=0.05) as determined by logistic regression.

Treatment	n	Trapped	Funnel	Downstream	Electric Field
OFF	22	32% a	36% a	14% a	18% a
Low	65	48% a	32% a	6% a	14% a
Medium	100	47% a	43% a	4% a	6% b
High	73	45% a	47% a	3% a	5% b

Table S8
Behavioral responses of rainbow trout (25 – 36 cm) in a raceway to the vertical electrode pulsed direct current field that blocked sea lamprey. The table lists the number of times rainbow trout moved into the electric field, passed upstream of the electric field and the number of times rainbow trout were stunned and paralyzed in the electric field.

Setting	Trials	Electric field	Upstream of field	Stunned	Paralyzed
OFF	5	119	53	0	0
2	5	54	0	3	1

Table S9
Behavioral responses of rainbow trout (25 – 36 cm) and white suckers (15 - 20 cm) in a raceway to the vertical electrode pulsed direct current field that resulted in the highest capture rate of sea lamprey. See Table S4 for descriptions of column headings.

Species	Setting	Trials	Upstream	Stunned	Paralyzed	Deflection rate	Passage Rate	Trapped (n)	Capture rate
Rainbow Trout	Off	5	123	0	0	7%	44%	2	2%
Rainbow Trout	7	5	57	12	3	7%	4%	2	4%
White Sucker	Off	5	25	0	0	0%	32%	10	40%
White Sucker	7	5	20	2	1	5%	5%	4	20%

Table S10
Longevity and injuries to rainbow trout, white suckers, and sea lampreys after 5 s exposure to the vertical electrode pulsed direct current field used to guide sea lampreys to a trap. Number (n) of rainbow trout, white suckers, and sea lampreys exposed to the electric field when turned off and activated at the medium and high settings described in the Ocqueoc River trapping trials (Fig. S6). Reported is the average weight and length of fish that were exposed to each treatment, the average number of days that fish survived after exposure (longevity) with the maximum possible longevity of 7 days because those fish surviving to day 7 were sacrificed, dissected, and inspected for internal injury. Bruising, hemorrhaging, bruised eye, and scar are the number of fish in each treatment documented with those injuries during dissection. Treatments with the same letter within species were not significantly different as determined by general linear (longevity) and generalized linear models (bruising, hemorrhaging, scar).

Treatment	**Species**	**n**	**Weight (g)**	**Length (mm)**	**Longevity (Days)**	**Bruising**	**Hemorrhaging**	**Bruised Eye**	**Scar**
Off	Rainbow Trout	15	392	335.2	6.8 a	2 a	4 a	0	0
Medium		15	421	343.3	7.0 a	1 a	4 a	1	0
High		15	419	344.7	6.6 a	3 a	3 a	0	2
Off	White Sucker	15	364	157.1	4.9 a	7 a	2 a	0	3 a
Medium		15	297	145.5	5.5 a	8 a	3 a	0	4 a
High		15	379	154.5	5.2 a	12 b	4 a	2	5 a
Off	Sea Lamprey	15	236	465.9	4.9 a	1	0	0	5
Medium		15	239	468.6	5.1 a	0	0	1	0
High		11	230	462.5	4.6 a	0	0	2	1

Supplementary Figures

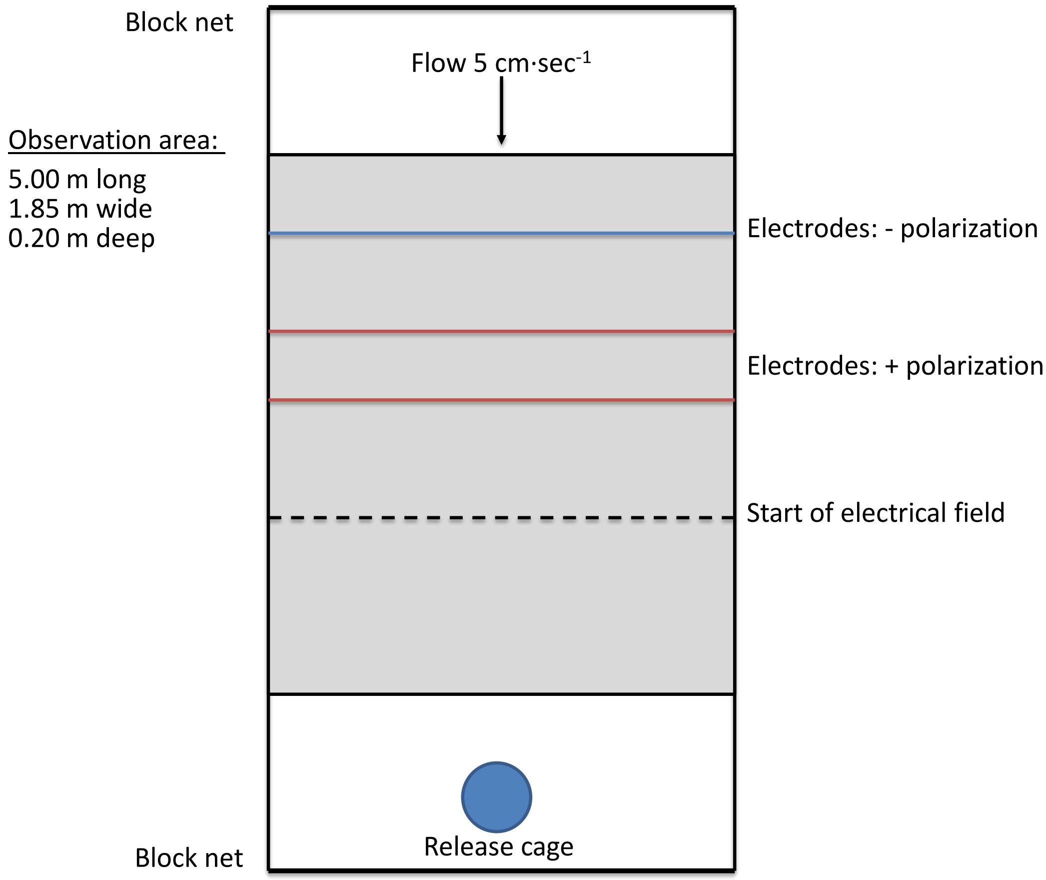


Fig. S1. Overhead view of the vertical electrode pulsed direct current field positioned as a non-physical barrier to fish migration. The shaded region of the raceway was monitored with a night-vision overhead camera. Positive electrode locations are illustrated with red lines and negative electrode locations with a blue line. The start of the electric field is illustrated with a dashed line (>0.1 V cm^{-1}). The highest voltage gradients occurred between positive and negative electrodes. Experimental subjects were released 1 m downstream of the observation area and behaviors within the observation area were recorded. To keep experimental subjects in the vicinity of the observation area, a block net was located 0.5 m downstream of the release cage and 1.5 m upstream of the observation area.

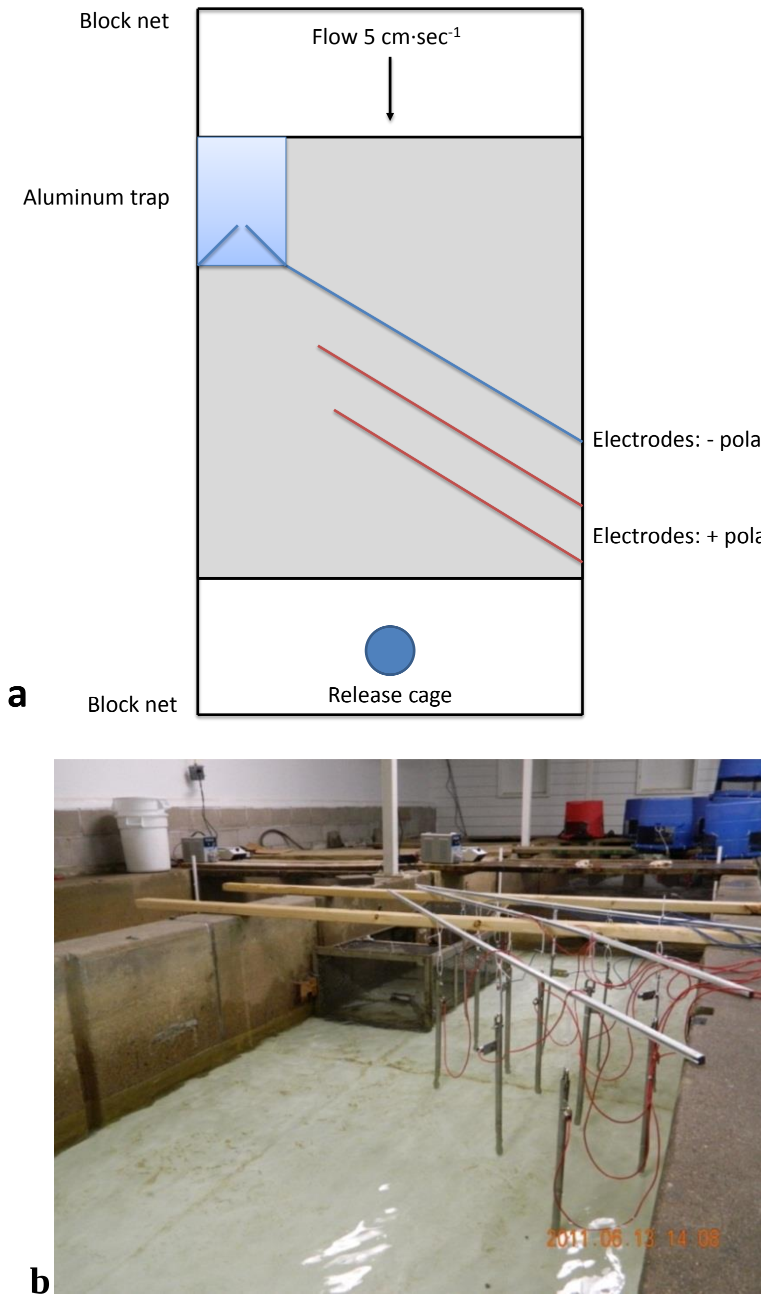


Fig. S2. The vertical electrode pulsed direct current field positioned as a non-physical trap lead to a sea lamprey trap in experimental raceway. Overhead view of the raceway set-up for electric guidance trapping experiments (**a**). The shaded region of the raceway was monitored with a night-vision overhead camera. Positive electrode locations are illustrated with red lines and negative electrode locations with a blue line. Electrodes were positioned to direct experimental subjects toward the aluminum trap, which in some treatments was polarized as a negative electrode. Sea lamprey were released 1 m downstream of the observation area and behaviors within the observation area were recorded. To keep sea lamprey in the vicinity of the observation area, a block net was located 0.5 m downstream of the release cage and 1.5 m upstream of the observation area. Photo of the pulsed DC trapping array showing that electrodes were suspended vertically in the raceway with overhead hangers (**b**).

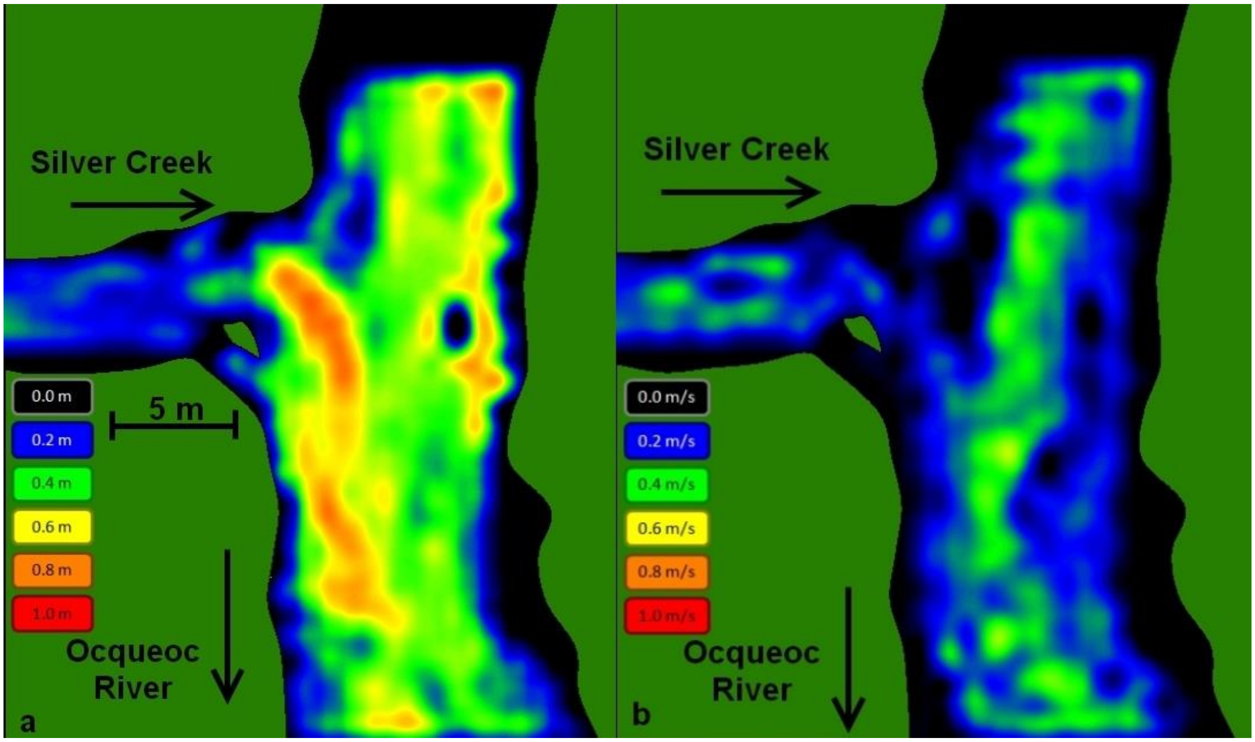
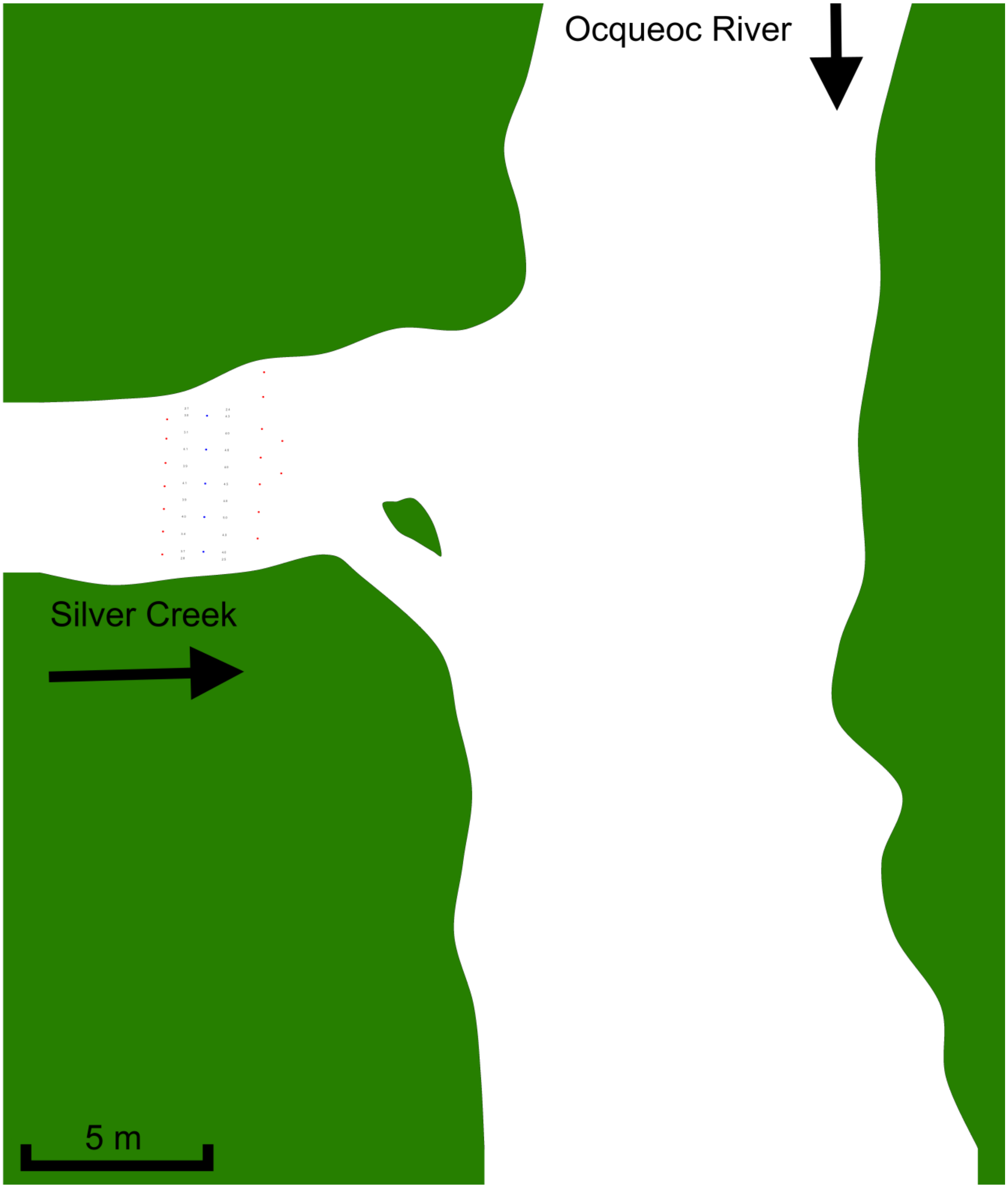


Fig. S3. The confluence of Silver Creek and the Ocqueoc River were vertical electrode pulsed direct current fields were tested to block and guide sea lamprey migration. Stream map illustrating depth (**a**). Stream map illustrating water velocity (**b**).

A



B

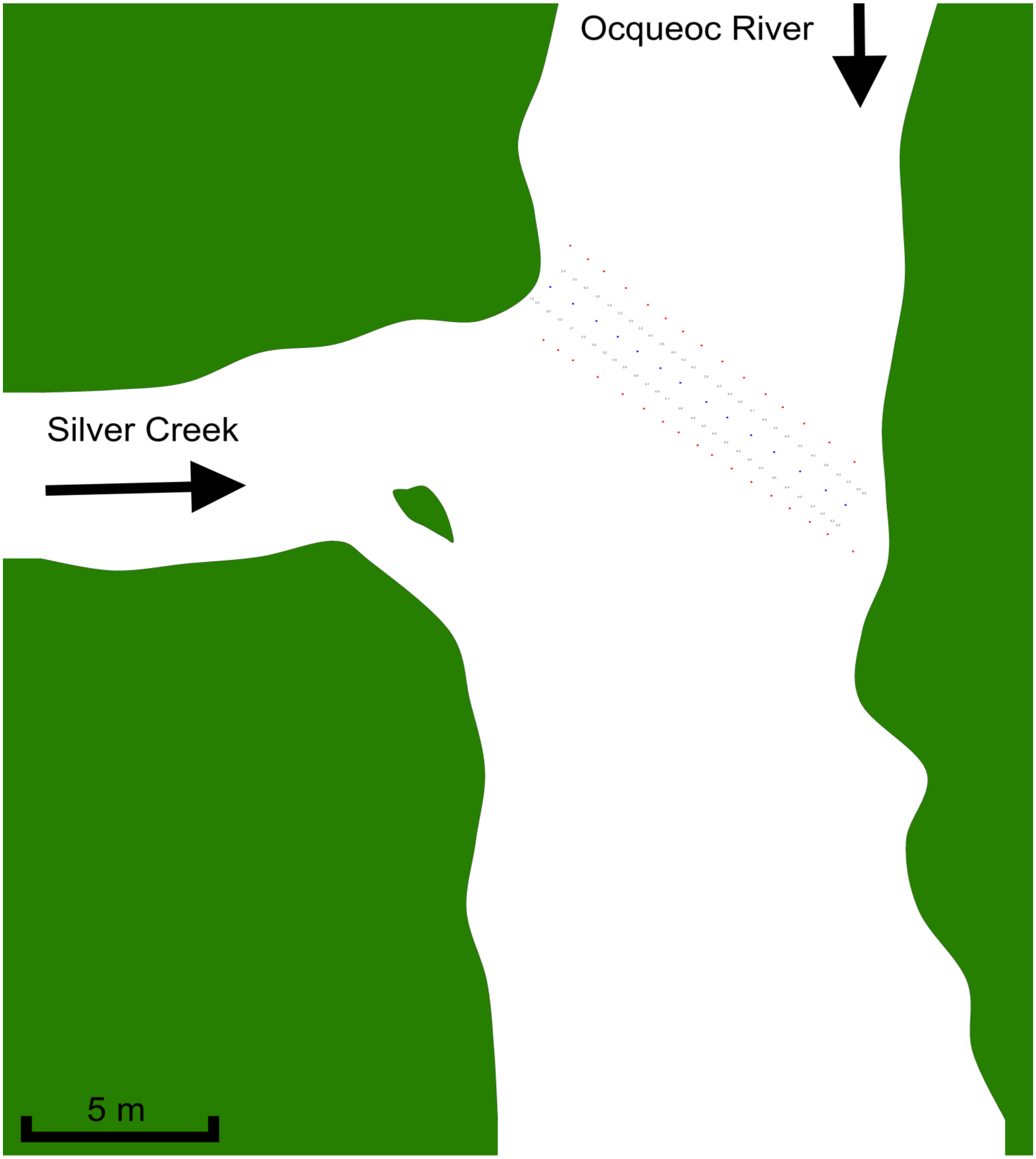
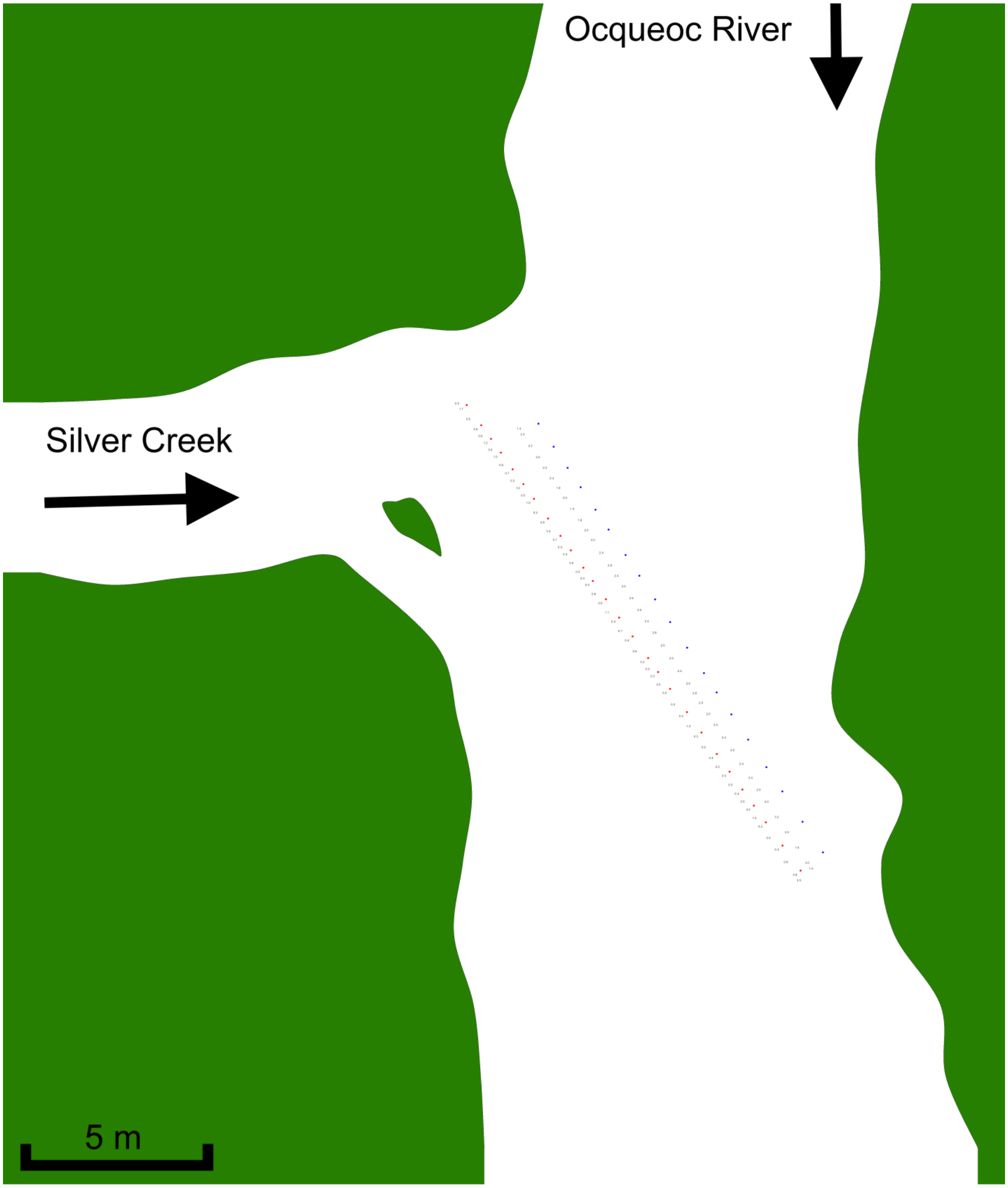


Fig. S4. Vertical electrode positions and voltage gradient (V cm^{-1}) of pulsed DC observed during sea lamprey blocking experiments. Electric field activated in Silver Creek (**A**). Electric field activated in the Ocqueoc River (**B**). Zoom in to see electrode locations and voltage gradient measurements at the location they were measured. Red dots are positive electrode positions. Blue dots are negative electrode positions.

A



B

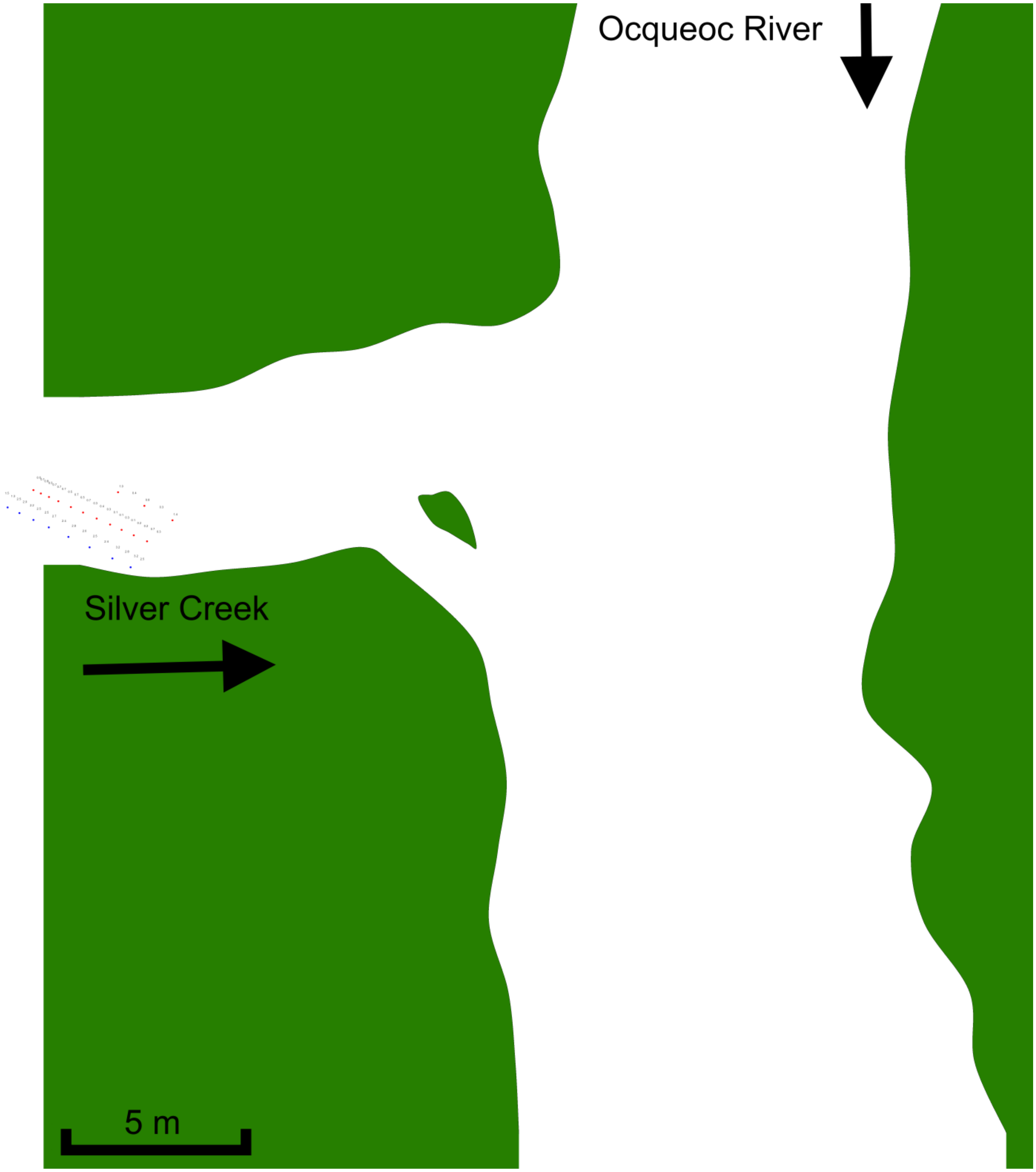
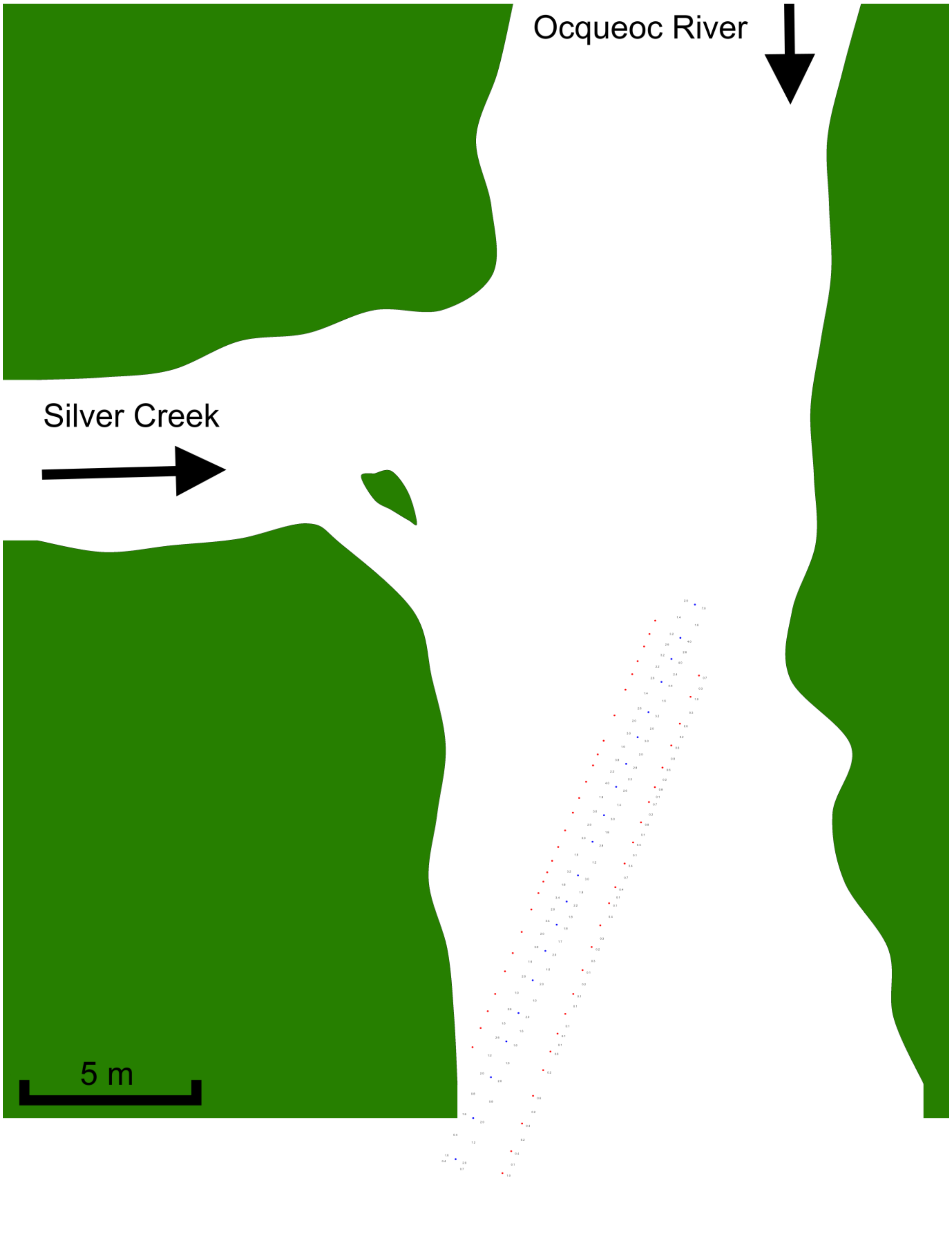


Fig. S5. Vertical electrode positions and voltage gradient (V cm^{-1}) of pulsed DC observed during sea lamprey trapping experiments in Silver Creek. Ocqueoc River electrical lead (**A**). Silver Creek electrical lead (**B**). Zoom in to see electrode locations and voltage gradient measurements at the location they were measured. Red dots are positive electrode positions. Blue dots are negative electrode positions.

A



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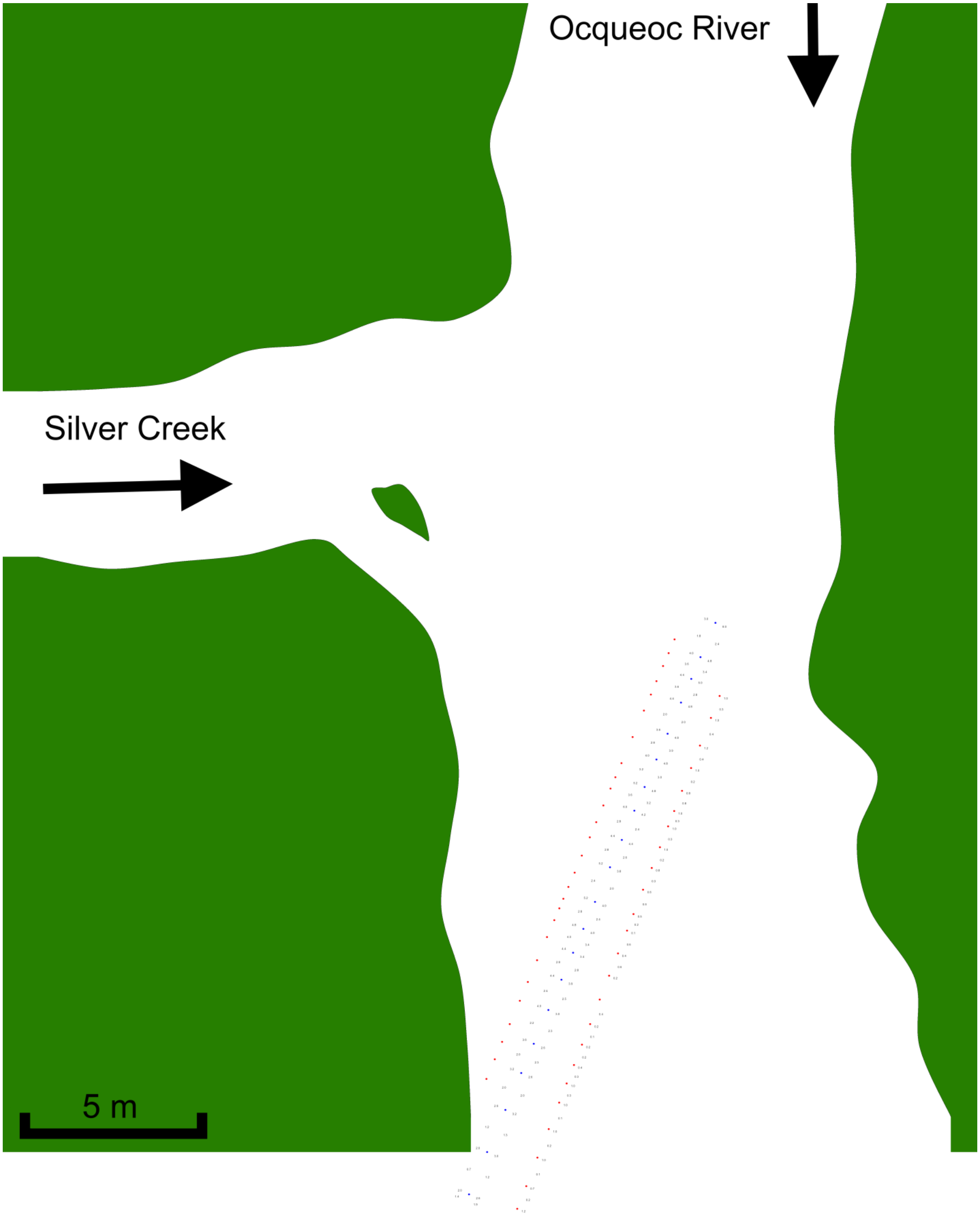

C

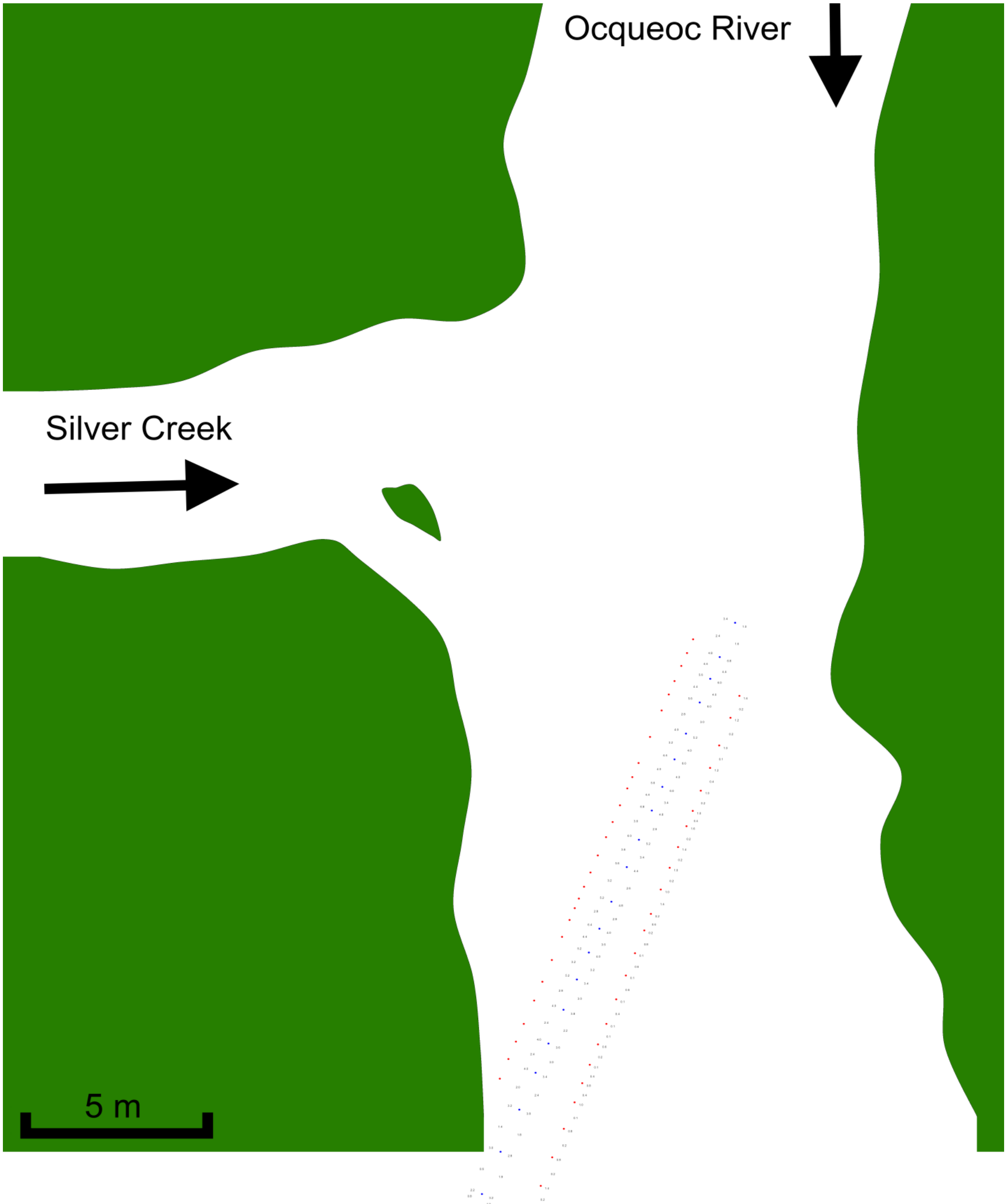

Fig. S6. Vertical electrode location and voltage gradient (V cm^{-1}) of pulsed DC observed during sea lamprey trapping experiments in Ocqueoc River. Low (**A**), medium (**B**), and high (**C**) setting. Zoom in to see electrode locations and voltage gradient measurements at the location they were measured. Red dots are positive electrode positions. Blue dots are negative electrode positions.